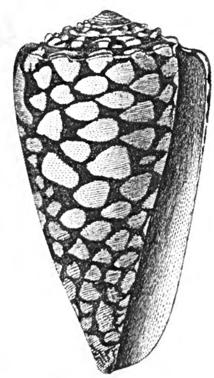

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Radula tooth turnover in the chiton *Acanthopleura hirtosa* (Blainville, 1825) (Mollusca: Polyplacophora)

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Abstract

The rate of radula production in the chiton *Acanthopleura hirtosa* (Blainville, 1825) was determined by following structural irregularities induced in the radula using a cold-shock treatment of 4°C for 48 h. In animals treated in this manner and subsequently maintained in an artificial intertidal habitat to ensure, as far as possible, a natural feeding regimen, the rate of radular production was calculated as 0.36 rows per day. This indicates that *A. hirtosa* renews its total radular length (mean 78 rows, SD = 6.5, n = 23) approximately once every 6.5 months, a relatively slow rate when compared with that of other molluscs.

Additional keywords: biomineralisation, cold-shocking, mollusc.

Introduction

The chiton radula consists of a ribbon like series of transverse tooth rows that are produced in a 'conveyor belt' manner (Lowenstam and Weiner 1989) from odontoblasts at the posterior end of the radula sheath (Kaas *et al.* 1998). Depending on the species, each transverse row consists of between 13 and 17 individual teeth. However, the main teeth that are involved in feeding are the prominent, glossy-black second lateral teeth, usually termed the major laterals. These teeth undergo a process of maturation along the length of the radula that involves the incorporation of iron and calcium based minerals onto an organic matrix (Kirschvink and Lowenstam 1979; Kim *et al.* 1989). This imparts to the teeth a unique combination of hardness and resilience, suitable for grazing on hard substrata (Webb *et al.* 1989). The anterior most teeth are worn by abrasion as the animals graze (Bullock 1989) and, as such, replacement appears to be in a state of dynamic equilibrium, where the rate of teeth being shed anteriorly is balanced by their production posteriorly (Runham 1963).

While a number of studies have been conducted in relation to the turnover rate of the molluscan radulae (Runham 1962, 1963; Runham and Isarankura 1966; Isarankura and Runham 1968; Padilla *et al.* 1996;), these have concentrated on gastropods, with a particular emphasis on pulmonates. Isarankura and Runham (1968) have developed a number of methods for studying the turnover rate, ranging from direct counts of teeth found in the faeces of animals, to marking the radula by surgical methods. These investigators also discovered that radula abnormalities occurring in *Helix aspersa* Möller, 1774, due to cold winter conditions, could be induced experimentally by a 'cold-shocking' technique. This method has since been found to be simple and reliable and facilitates the testing of a large number of individuals (Padilla *et al.* 1996).

The ongoing interest in the biomineralisation process in chiton teeth (see, for example, Webb *et al.* 1989; Lee *et al.* 1998, 2000) has led to the need to estimate the rate of tooth turnover, so that the demand for mineral precursors can be ascertained and some estimate of the flux of these elements through the chiton body established. The species used in the

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present study was *Acanthopleura hirtosa* (Blainville, 1825), which is an abundant member of the Western Australian molluscan community. It occurs in the upper intertidal region of coastlines from Albany to Shark Bay (Wells and Bryce 1986) and has proved to be an ideal model for studies of the biomineralisation process (Evans *et al.* 1990, 1992; Macey and Brooker 1996; Macey *et al.* 1996).

Materials and methods

Adult specimens (mean length 37.6 ± 4.8 mm, $n = 36$) of *A. hirtosa* were collected from various sites in the Perth metropolitan area (Lat. 32°S, Long. 116°E) between February and March 2001. To reduce the likelihood of any damage to the specimens during collection, chitons were removed from their home scars by driving a screwdriver into the substratum near the mantle of each specimen. Each animal, along with a portion of the substratum to which it was attached, was levered free of the rock surface, placed in fresh seawater and transported back to the laboratory as quickly as possible.

To minimise the chances of the study altering the natural rate of radula production, all experimental animals were kept in an artificial environment, or 'mesocosm'. This consisted of a large open air tank containing limestone rocks collected from the intertidal region normally occupied by *A. hirtosa*. The rocks were positioned in the tank such that they partially protruded above the water line, providing the chitons with a habitat approximating their natural intertidal environment. In order to keep the exposed rocks moist and to simulate surf spray, the tank was continuously supplied with fresh seawater that was delivered via an overhead reticulation system. No organisms were removed from the rocks, which contained various species of algae, anemones, limpets, barnacles, crabs, polychaetes and other small invertebrate fauna. A number of juvenile and small adult chitons of various other species were also present.

In order to test the viability of the mesocosm as a chiton habitat, it was initially seeded with 21 specimens of *A. hirtosa* collected from the wild in early February and left to reside for a period of 2 months. Ten of these animals were included in the cold-shocking procedure, along with a further 15 collected from the wild in late March. Differentiation of the freshly collected specimens from the control animals was achieved by using a Dremel (Racine, Wisconsin, USA) engraving tool to score lines on either the fourth or fifth valve, respectively. All 25 animals were then subjected to a derivation of the cold-shocking technique of Isarankura and Runham (1968). A constriction was produced in the developing radula membrane by plunging the chitons into seawater prelowered to a temperature of 4°C and maintaining them at that temperature for 48 h. Directly following the cold-shocking procedure, while the animals were in a relaxed and extended state, their lengths were recorded. Two specimens were dissected and their radulae removed in order to provide Day 0 data, whereas all remaining specimens were transferred to the mesocosm, where they attached to the substratum. On subsequent alternate days, at the same time each day (± 2 h), a single specimen was selected at random for dissection. Prior to removal of the radula, chitons were anaesthetised by placing them in a shallow container of fresh tap water, which was then chilled at −1°C for 1 h. Radulae were then dissected out, cleaned using 2.5% sodium hypochlorite and the radula length and total number of transverse rows recorded. Radula constriction was observed and photographed using an Olympus DP10 digital camera, attached to an Olympus SZH10 stereo dissecting microscope, and the number of teeth prior to the position of the constriction was counted and recorded. In order to verify that the constriction anomaly was not a natural construct of the radular ribbon, five chitons were dissected straight from the wild for comparison.

Results

No constrictions were found in the radulae of animals dissected fresh from the field, indicating that the observed deformations were attributable to the cold-shocking procedure rather than being a natural construct of the radula. Only a single animal died in the mesocosm during the initial 2-month viability study. This occurred within a few days of transfer, suggesting that the combined shock of collection and transfer was the cause of death. A further two animals died following the 4°C cold-shocking procedure and transfer to the mesocosm. Animals that survived were assumed to be feeding in a normal manner due to the maintenance of limited algal coverage on the substratum and the deposition of a large number of faecal pellets in the mesocosm. Indeed, following the experimental period,

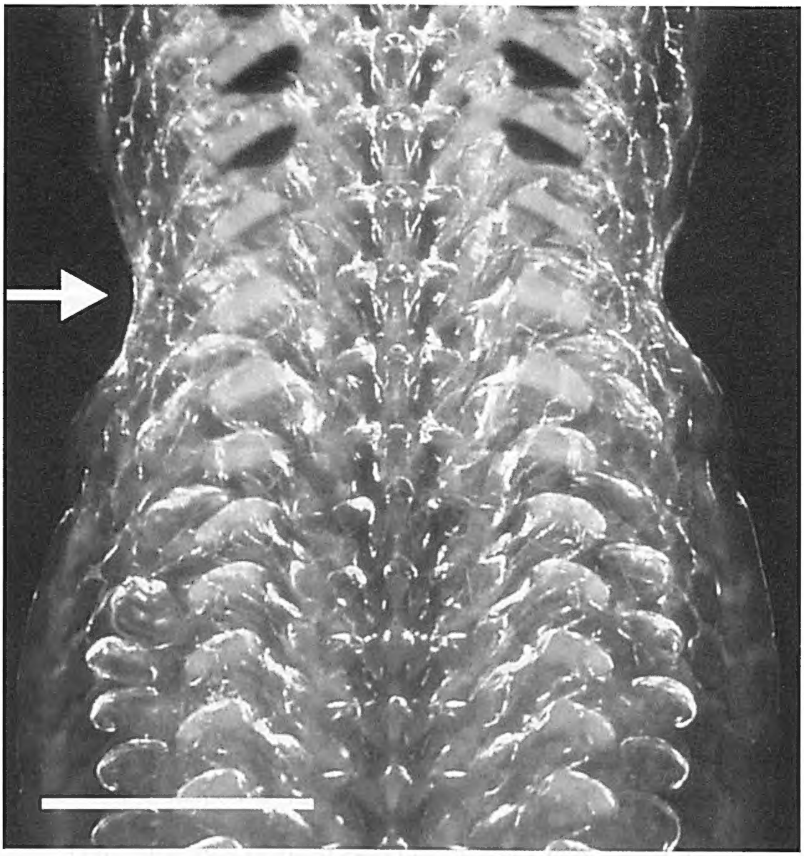

Fig. 1. Constriction (arrow) produced in the radula by placing animals in seawater precooled to a temperature of 4°C and maintaining them at that temperature for 48 h. Scale bar: 1 mm.

some of the smaller chiton species from the mesocosm were found to have spawned, indicating that these chitons, at least, were capable of reproducing while in the system. Preliminary cold-shocking trials at a temperature of −1°C produced 90% mortality, suggesting that this lower temperature is beyond the tolerance limit of this species.

The cold-shocking technique produced an obvious constriction of the radula membrane that could be tracked along the radula in all experimental animals throughout the experimental period (Fig. 1). Whereas some individual variation was seen in tooth turnover rate towards the end of the experimental period, the overall results were very consistent and allowed the calculation of an average rate of tooth turnover of 0.36 rows per day (SD = 0.06, $n = 20$; Fig. 2). Initial determination of the position of the constriction with regard to tooth row number was made difficult by the very low turnover rate, which meant that fractions of tooth rows had to be estimated. However, there does appears to be an initial lag phase, because the mean turnover rate for the first 8 days is only 0.27 rows per day (SD = 0.04, $n = 4$), which could be attributable to recovery from the cold-shocking procedure. Data obtained from animals in the study indicate that the average total number of transverse tooth rows for *A. hirtosa* is 78 (SD = 6.5, $n = 23$). Combining the data for tooth turnover rate and total row number gives a total radula replacement time of approximately 203 days (~6.5 months).

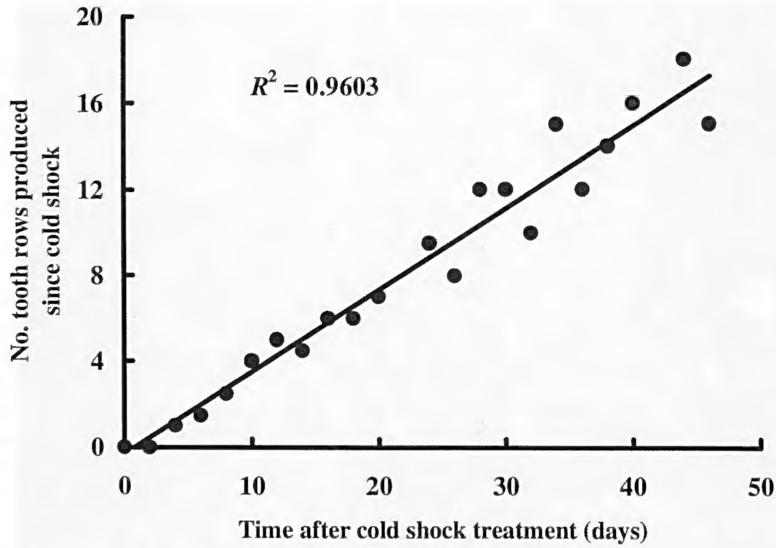

Fig. 2. Number of tooth rows formed after cold shock treatment.

Discussion

This paper reports, for the first time, the use of a cold-shocking method for measuring tooth turnover rate in temperate intertidal chitons, revealing a radula replacement rate of 0.36 rows per day in *A. hirtosa*. A previous study of radula production, using a variety of techniques including cold-shocking, found that radula turnover rates of 15 prosobranch and pulmonate species varied from 1 to 6.4 tooth rows per day (Isarankura and Runham 1968). In a subsequent study of two littorinid species, the cold-shocking technique revealed a calculated turnover rate of approximately 2.95 rows per day (Padilla *et al.* 1996). Isrankura and Runham (1968) found that a number of factors affect tooth turnover rate in gastropods, none more profound than that of ambient temperature, which increased radula production two to threefold in response to incremental rises of 10°C. The Perth region experiences a 'Mediterranean' climate, with average maximum and minimum temperatures of 29 and 18°C, respectively, in summer and 18 and 9°C, respectively, in winter. Local nearshore water temperatures range from 15 to 24°C, from winter to summer, respectively (Pearce *et al.* 1999). The present study was conducted during the months of late summer to early autumn, with the mesocosm at a relatively high water temperature of 22°C, with a variation of less than 1°C overnight. Hence, the production rate of 0.36 rows per day, although low in comparison with the gastropod species of previous studies, is likely to reflect a relatively high turnover rate for *A. hirtosa*. It would be interesting to repeat the study during the winter months to determine whether the radula turnover rate is reduced at a lower temperature. Isarankura and Runham (1968) found that active herbivores have higher rates of radula production than more sluggish or carnivorous forms, indicating that turnover is adapted to the feeding activity of the animal. Although it is difficult to compare the level of feeding intensity between gastropods and *A. hirtosa*, it can be argued that because *A. hirtosa* is an intertidal species that has an intermittent, semidiurnal feeding regimen, it is not an active herbivore for much of each 24 h period. As such, this could account, in part, for its comparatively low turnover rate.

There are several other factors that could affect the wide variation exhibited in the turnover rates of the different molluscs studied, including the physical size of the teeth, their structural design, their resistance to wear and the hardness of the animal's food source. The initial size of the mature teeth, prior to their use in feeding, determines how quickly they will wear away, with smaller teeth becoming functionally ineffective and in need of replacement sooner than larger teeth. Unfortunately, the lack of any data on tooth size in previous studies precludes direct comparison with the chiton teeth in the present study. However, the main teeth used by chitons in feeding, the second laterals, are usually large prominent teeth. In *A. hirtosa*, the cusps of these teeth measure 254 μm high and 247 μm wide (SD = 4.7, 3.9, respectively; $n = 8$). Hence, it may well be that the possession of large cusps affords the chiton a slower rate of tooth wear.

The majority of gastropods in the studies of both Isrankura and Runham (1968) and Padilla *et al.* (1966) were herbivores feeding off seaweeds, soft algae or lettuce. The only species that has a natural feeding strategy similar to that of *A. hirtosa* is *Patella vulgata*. Both species are hard substrate grazers, and although *P. vulgata* was not given a natural substrate to feed off, at approximately 1.5 rows per day it returned one of the lowest radula turnover rates for the gastropods (Isrankura and Runham 1968). This is somewhat contradictory to what would be expected, because it could be assumed that the abrasive, high impact nature of chiton and limpet feeding would actually necessitate a high turnover rate. However, another factor that both these species have in common is the incorporation of hard minerals into their tooth design, which affords them greater resistance to wear. The main working teeth of *A. hirtosa* are hardened with iron oxides, such as magnetite and lepidocrocite (Kim *et al.* 1989; Lee *et al.* 1998), whereas *P. vulgata* incorporates iron and silicon into its teeth (Lowenstam 1962, 1971). As such, it could be suggested that radula turnover in chitons and limpets is slower than that found in other molluscan groups due to the reduced mechanical wear of the teeth afforded by their extensive mineralisation. A further point to consider is that mineralisation is a physiologically expensive process, which necessitates rationalisation of tooth production rates with respect to the total energy allocation of radula manufacture.

The only other published study on radula production rates in the polyplacophora was that performed by Nesson (1969), where the rate of radula replacement for *Mopalia muscosa* (Gould, 1846) was determined by labelling the teeth with ^{59}Fe. In that study, the tooth turnover rate was calculated to be approximately 0.6 rows per day, nearly double that of *A. hirtosa*. However, this is still considerably slower than the rates calculated for the gastropod species, suggesting that the polyplacophora, as a group, may have slower radula production rates than other mollusc groups. Whether this reduced rate can be attributed to their mineralisation process remains to be seen and further research into radula production may provide insights into the tooth hardness–turnover rate association.

The difference in the rates observed between *A. hirtosa* and *M. muscosa* may lie in the differing tooth morphology and feeding regimens of these two species. The working face of the major lateral teeth in chitons varies in structure from a broad chisel-like form (as in the chitonidae) to one to three pronounced cusps (in most other chiton families) (Nesson and Lowenstam 1985). The cusp structure seen in *A. hirtosa* is of the broad unicuspid type (Macey *et al.* 1996), whereas that of *M. muscosa* is of a tricuspid design (Nesson 1969). While no direct comparison has been made between these two species, comparisons of the structural organisation of the cusps of chiton teeth have been made between *A. hirtosa* and *Plaxiphora albida* (de Blainville, 1825), which also has tricuspid teeth (Macey *et al.* 1996). The two cusp designs are used differently with respect to feeding, with the major laterals of

P. albida used in a rake-like manner, whereas those of *A. hirtosa* have a more excavational capacity (Macey *et al.* 1996). From this feeding strategy, it would be expected that the teeth of *A. hirtosa* would be worn away more quickly. The fact that this does not occur may well be attributable to differences in tooth structure at the microcrystalline level.

A number of factors may be responsible for the slight variation seen in rates of tooth row formation for individual specimens of *A. hirtosa*. Isarankura and Runham (1968) found a close correlation between radula replacement and the age of very young specimens of the gastropod *Achatina fulica* (Bowdich, 1822), whereas in older specimens the rate appears to be more closely related to the size of individuals. Although only adult chitons were used in the present study, there was a difference of 16 mm in length between the largest and smallest specimens, so size cannot be ruled out as a factor. Perhaps of greater significance to the individual variation is the effect of temperature on metabolism, because any fluctuations may have slowed or increased radula production over the course of the study. While the ambient temperature of the artificial mesocosm was relatively constant for the experimentation period, and day to day variations would be expected to have a compound effect that should be similar for all chitons in the experiment, the location of individual chitons within the mesocosm may have caused some variation. Because some of the rocks were submerged and others exposed, some chitons may have adopted positions that were sheltered from the elements, whereas others may have been subjected to a more variable range of conditions with regard to temperature and water availability.

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A review of the Indo-Pacific *Lioconcha* Mörch (Mollusca : Bivalvia : Veneridae), including a description of four new species from Queensland, New Caledonia and the Philippine Islands

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Abstract

The Indo-West Pacific venerid genus *Lioconcha* is reviewed, with special emphasis on species occurring in the Australian and New Caledonian regions. Nineteen species, including four new species, are recognised: *Lioconcha castrensis* (Linnaeus, 1758), *L. macaulayi* n. sp., *L. hieroglyphica* (Conrad, 1837), *L. tigrina* (Lamarck, 1818), *L. fastigiata* (Sowerby, 1851), *L. annettae* Lamprell & Whitehead, 1990, *L. pseudofastigiata* n. sp., *L. ornata* (Dillwyn, 1817), *L. berthaulti* n. sp., *L. sowerbyi* (Deshayes, 1853), *L. polita* (Röding, 1798), *L. schioettei* n. sp., *L. trimaculata* (Lamarck, 1818), *L. philippinarum* (Hanley, 1844), *L. dautzenbergi* (Prashad, 1932), *L. melharteae* Lamprell & Stanisic, 1996, *L. caledonensis* Harte & Lamprell, 1999, *L. richerdeforgesi* Lamprell & Stanisic, 1996 and *L. gordoni* (E. A. Smith, 1885). Colour variation within species ranges from very high (*L. ornata*, *L. castrensis*) to very low (*L. melharteae*, *L. caledonensis*, *L. philippinarum*). All species are figured, diagnosed and discussed and a key is presented. Types of the following taxa are also figured: neotype of *Venus ornata* Dillwyn, 1817; holotypes of *Lioconcha berthaulti* n. sp.; *L. macaulayi* n. sp.; *L. pseudofastigiata* n. sp.; *L. schioettei* n. sp.; *L. annettae* Lamprell & Whitehead, 1990; *Cytherea tigrina* Lamarck, 1818; *Hysteroconcha* (?*Lamelliconcha*) *dautzenbergi* Prashad, 1932 and *Cytherea sulcatina* Lamarck, 1818; lectotypes of *Cytherea hebraea* Sowerby, 1851 and *Circe sowerbyi* Deshayes, 1853. Lectotypes of *Cytherea hieroglyphica* Conrad and *C. fastigiata* Sowerby are based on original figures, in the absence of other undoubted type material. Subdivision of *Lioconcha* into two subgenera (*Lioconcha sensu stricto* and *Sulcilioconcha*), based solely on the presence or absence of concentric ridge sculpture, appears unwarranted.

Introduction

Species of the genus *Lioconcha* Mörch, 1853 are among the more difficult of the Veneridae to identify because of their sometimes wide variation in colour pattern and the vestigial nature of the pallial sinus, the latter structures widely used as a valuable species diagnostic elsewhere within the Veneridae. Species of *Lioconcha* are usually characterised by bright, sometimes intricate shell colour patterns and a smooth shell. Species are known from tropical and subtropical regions of the Indo-West Pacific, but have yet to be reported from the eastern Pacific or the Atlantic. They are infaunal, occurring in clean, muddy or coral sand, typically in sheltered shallow water habitats and, sometimes, in moderately deep water (>100 m; Lamprell and Stanisic 1996). *Lioconcha* shells are commonly collected either as beached specimens or in the vicinity of octopus dens, but living material can usually only be gathered by dredging or digging into the sediment.

Although *Lioconcha* from New Caledonia (Lamprell and Stanisic 1996) and South Africa, Mozambique and the Mascarene and Andaman Islands (Lamprell and Kilburn 1999*a*,*b*) have been previously discussed, the genus as a whole has not been reviewed in the modern literature. In the present study, we diagnose or describe all known species of extant *Lioconcha* and take the opportunity to briefly evaluate the relationships within the genus based on shell features and available distribution data. Particular emphasis is given to

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recently collected material from Queensland, the Philippine Islands and New Caledonia held in the Australian Museum (Sydney, NSW, Australia), the Queensland Museum (Brisbane, Qld, Australia) and Muséum National d'Histoire Naturelle (Paris, France) in addition to specimens from private collections.

Methods

Shell dimensions

For all material examined, length is the greatest distance between the anterior and posterior extremities, height is measured vertically from the umbo to the ventral margin and total width (inflation or breadth) is the greatest distance between the external surfaces of the paired valves. Unless stated otherwise, measurements are given for the largest specimen examined by the authors.

Abbreviations

lv, left valve
pv, paired valves
rv, right valve.

Institutional abbreviations

AMNH, American Museum of Natural History
AMS, Australian Museum, Sydney
BMNH, Natural History Museum, London
KL, Lamprell Collection
MNHN, Muséum National d'Histoire Naturelle, Paris
MNHG, Muséum d'Histoire Naturelle, Geneva
NM, Natal Museum
NMW, National Museum Wales
NTM, Northern Territory Museum of Art and Sciences, Darwin
QM, Queensland Museum, Brisbane
ZMUC, Zoological Museum, University of Copenhagen, Denmark

Systematics

Superfamily **VENEROIDEA** Rafinesque, 1815

Family **VENERIDAE** Rafinesque, 1815

Subfamily **PITARIINAE** Stewart, 1930

Genus ***Lioconcha*** Mörch, 1853

Type species: *Venus castrensis* Linnaeus, 1758 (by subsequent designation of Stoliczka, 1870).

Diagnosis

Equivalve; resembling *Pitar* but with pallial sinus vestigial; valves rounded to elongate–trigonal, moderately to well inflated with strongly developed veneroid hinge dentition (prominent cardinal and lateral teeth); lunule flat to raised, heart or tear-drop shaped with margin strongly to weakly incised; periostracum usually thin, but sometimes thick peripherally in large adults; externally smooth to glossy with only sculpture consisting of concentric growth lines or striae, often supplemented by variously developed concentric ridges (especially at ventral and /or anterior and posterior margins); exterior coloration typically with zigzag or triangular patterning, sometimes supplemented or replaced by one

or more rays originating umbonally; internal colouration within genus variable, but usually species specific (usually white, but often with yellow, brown or purple patches).

Lioconcha castrensis (Linnaeus, 1758)

(Figs 1*A–K*, 12*A*, 15*A*)

Venus castrensis Linnaeus, 1758: 687 (type locality: 'in O. utriusque Indiae' (= 'both East and West Indies'); Chemnitz, 1782: figs 367–370; Chemnitz, 1788: fig. 1662.
Venus fulminea Röding, 1798: 181, no. 295 (based on Chemnitz, 1782: figs 369–370).
Venus lorenziana Dillwyn, 1817: 184 (based on Chemnitz, 1788: figs 1961–2).
Cytherea ornata Lamarck, 1818: 578 (refers Chemnitz, 1782: figs 369–370) (not Dillwyn, 1817); Lamy & Fischer-Piette, 1937: 273.
Cytherea castrensis (Linnaeus). Sowerby, 1851: sp. 103; Lamy & Fischer-Piette, 1937: 273.
Circe castrensis (Linnaeus). Reeve, 1863: pl. 7.
Lioconcha castrensis (Linnaeus). Römer, 1864–69 (1868): 44; Lamy, 1930: 135; Abbott & Dance, 1982: 359, fig. 6; Springsteen and Leobrera, 1986: 297, pl. 85 fig. 2.
Lioconcha lorenziana (Dillwyn). Habe, 1977: 259; Abbott & Dance, 1982: 359, fig. 9.
Lioconcha (*Lioconcha*) *castrensis* (Linnaeus). Habe, 1977: 258; Oliver, 1992: 185, pl. 40, fig. 1*a*,*b*; Lamprell & Whitehead, 1992: sp. 543; Lamprell & Stanisic, 1996: 30, fig. 1*g*,*h*; Lamprell & Kilburn, 1999*b*: 43, pl. 1, figs *a*,*b*.
Lioconcha tigrina. – Eisenberg, 1981: 151, fig. 3-3*a* (not of Lamarck, 1818).

Material examined

Spengler collection, Ostindien. Specimen figured by Chemnitz (1782: fig. 367; see fig. 1*H*,*I* herein), ZMUC; Spengler collection, South Seas. Specimen figured by Chemnitz (1782; specimen named *V. lorenziana* by Dillwyn (1817), fig. 1662; see Fig. 1*J*,*K* herein), ZMUC. **Australia: Queensland**: Little Trunk Reef, lagoon, AMNH.303314 (2pv); trawled 10 m off Palm Island, AMNH.303127 (2pv); dredged 8 m, Herald Prong Reef, no. 2, Swains Reef, AMNH. 303936 (1pv); on sand bar, Bowling Green Bay, Townsville, AMNH.303939 (1pv); Batt Reef; AMNH.303272 (1pv); trawled in lagoon Slasher's Reef no. 1, AMNH.303035 (1pv); 1–2 m, in sandy coral, Opal Reef, north of Cairns, 16°15′S, 145°50′E, AMS C.356686 (3pv) (preserved); Swains Reef, AMS C.148179 (2lv, 1rv); Murray Island, Torres Strait, AMS C.29811 (3pv); Ribbon Reef, 4.5 m, AMS C.137968 (1pv); Macgillivray Cay, Swains Reef, 17 m, AMS C.105190 (1pv); Ellison Reef, AMS C.117393 (1pv); Lady Musgrave Island, AMS C.94051 (1pv); trawled Lady Musgrave lagoon, QM MO.34152 (5pv); Tryon Island (beach), QM MO,31762 (1rv); Darnley Island, Torres Strait, QM MO.8521 (3rv, 2lv); Murray Island, Torres Strait (beach), QM MO.10569 (2rv, 3lv). **Western Australia**: 10 m, Hibernia Reef, Timor Sea, NTM P.7541 (1pv); **Cocos Island**: AMS C.119593 (1lv, 1rv). **Papua New Guinea**: 5–6 m, in sand around coral shoal, between Kranket Island and Madang, 5°12′S, 145°50′E, AMS C.356678 (1pv) (preserved); Shoal to W of Kranket Island, Madang. Bougainville, AMS C 82973 (1pv); Gihili, AMS C.17410 (1pv). **West Irian**: N.Mios, Woendi Island, Padaido Islands, AMS C.96947 (1pv). **New Ireland**: Mangop, Manus Island, AMS C.98254 (4pv); **Admiralty Group**, AMS C.141373 (1pv). **New Hebrides**: Aneiteum, AMS C.1959 (1pv). **Fiji**: KL (1pv) **Suva**: Vitu Levu Island, NTM P.8787 (1rv). **New Hanova Island**: Metelaung Village, NTM P.1663 (1lv). **Loyalty Islands**: Ouvéa Atoll, NTM P.5792 (1lv). **New Caledonia**: Poum Bay, Daomboui Island, 0–3 m, in sand and coral, 20°9′S, 163°59′E, AMS C.356679 (in part) (3pv) (preserved); between Crouy and Abore Reef, 6 m, AMNH.303271 (4pv, 1lv); Crouy Reef, AMNH.303240 (1pv); Anse Vata, Noumea, AMS C.83706 (1pv) (note: for full New Caledonia collecting data, see Lamprell and Stanisic (1996)); Lifou, AMS C.3899 (1pv). **Tonga**: Tongakabu, AMS C.15069 (1pv). **Philippine Islands**: no localised data, AMNH.303128 (1pv); Mactan Channel, Visayas, AMS C.371092 (2rv); off Bunyong Boh, Mactan Island, 10°05′N, 124°00′E, 7–30 m, coral reef face, AMS C.141371 (1 pv, 1lv). **Solomon Islands**: Guadalcanal Island, AMS C.15068 (1pv); AMS C.52243 (1pv): **Indonesia**: Tanimbar Islands, NTM P.2417 (1 rv, 1lv). **Tanzania**. AMS C.368268 (1lv). **Israel**: Nuweiba, Sinai, AMS C.135652 (2rv). **Réunion**: off Souris Chaude, 60 m, sand, NM K.2782 (3lv, 1rv). **Mauritius**: off Trou aux Biches, reef front in 5 m, Sep 1991, NM K.8312 (1rv). **Red Sea**: specimen figured by Oliver (1992), pl. 40, figs 1*a*,*b*, NMW.1955.158.02272 (1pv).

Diagnosis

Shell round to ovate, solid and very thick, glossy, moderately to very inflated; umbones slightly to markedly prosogyrate (moreso in large adults); lunule heart-shaped to lanceolate, raised, well delineated by incised line; umbones low, slightly prosogyrate; anterodorsal margin sloping, widely convex terminally; ventral margin widely rounded; posterodorsal margin, sloping, widely convex. Sculpture of fine growth striae, supplemented by faintly raised ridges at the anterior and especially posterior extremities (ridges often wrinkled). Colour variable externally, usually white with patches of grey–pink overlain with blue–black to tan zigzag or chevron patterns, some specimens with hieroglyphic patterns (i.e. composed of variously shaped rod or broken chevron markings), umbones white, lunule white (sometimes with one or two lines of pattern), with very small brown–black spots umbonally; shell internally usually white, occasionally with pale peach medially. Shell length to 55 mm.

Distribution and habitat

Indo-West Pacific; loose coral sand, usually in reef lagoons.

Remarks

Lioconcha castrensis is the largest living species of *Lioconcha*, reaching a maximum of 55 mm in length. Because of its marked variability in terms of colour pattern, this species could be confused with species such as *Lioconcha fastigiata* (Sowerby) and *Lioconcha macaulayi* n. sp. However, there are reliable shell features for distinguishing these species from each other and from other members of *Lioconcha*. *Lioconcha castrensis* differs from *L. fastigiata* in its larger, more ovate and considerably thicker shell, a heavier hinge line (with more robust teeth) and a noticeably raised, well-defined lunule. *Lioconcha castrensis* differs from *L. macaulayi* in having a more ovate, heavier shell and in attaining a larger adult size. *Lioconcha castrensis* and *L. macaulayi* occur together in Lady Musgrave lagoon (Great Barrier Reef), New Caledonia (Anse Vata, near Noumea, Crouy Reef) and Saumarez Reef. Based on a consideration of shell features alone, the relationship between *L. castrensis* and *L. macaulayi* appears to be a close one. Although *L. hieroglyphica* (Conrad) has been considered a synonym of *L. castrensis* (Kay 1979; Lamprell and Stanisic 1996), it now seems to be a valid species, judging from Conrad's illustration (herein selected as the lectotype, because no type material of *L. hieroglyphica* has been located to date) and from our examination of three lots of Hawaiian material (held in the Australian Museum) that match Conrad's description and illustration (see also pp. 108–110 for further discussion). Dillwyn (1817) described *V. lorenziana* based on figures 1961 and 1962 in Chemnitz (1788) and remarked that 'The shell in size and form much resembles *V. castrensis*, of which it may perhaps be nothing but a variety; it is of a dirty white colour, with transverse irregular nearly parallel zic-zac reddish brown stripes'. Considering the wide variation in colour patterns among the numerous specimens we have examined and evident in the figures of Chemnitz from his monograph (Chemnitz 1788), we would agree with Dillwyn that this species is probably another variation of *L. castrensis*. However, as with *Lioconcha ornata* (Dillwyn), comparative anatomy and/or molecular studies would greatly assist in determining whether any of the various colour forms of *L. castrensis* deserve formal taxonomic recognition. As a starting point for such future work, we would

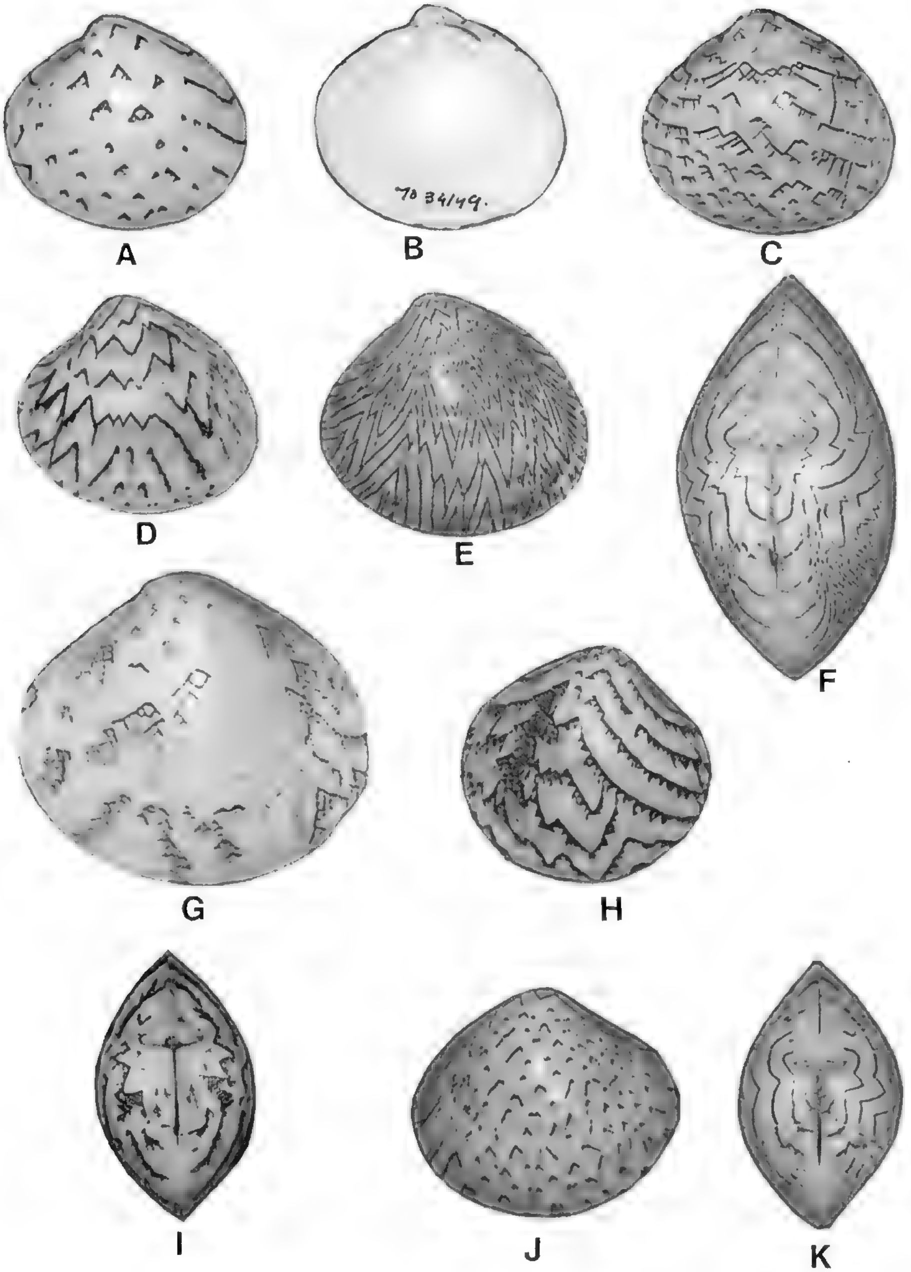

Fig. 1. *Lioconcha castrensis* (Linnaeus, 1758). *A,B*, Lady Musgrave lagoon, QM MO.34149, length 33.9 mm: *A*, external view lv; *B*, internal view rv. *C*, Philippine Islands, AMNH.303128, length 42.3 mm, external view lv. *D*, Little Trunk Reef Qld, AMNH.303314, length 48 mm, external view lv. *E,F*, Suva, Fiji, KL, length 54.5 mm: *E*, external view lv; *F*, dorsal view of pv. *G*, Swains Reef, Qld, AMNH.303936, length 35.2 mm, external view lv. *H,I*, Spengler collection, Ostindien, specimen figured by Chemnitz (1782: fig. 367), length 48 mm, height 45 mm, width of pv 28 mm: *H*, external view rv; *I*, dorsal view pv. *J,K*, Spengler collection, South Seas, specimen figured by Chemnitz (1782: fig. 1662; specimen named *Venus lorenziana* by Dillwyn), length 40 mm, height 35 mm, width of pv 24 mm: *J*, external view rv; *K*, dorsal view pv.

suggest a comparison of the typical *L. castrensis* (heavy zigzag markings) and the hieroglyphic form (of numerous, small, often broken tent markings).

Lioconcha macaulayi n. sp.

(Figs 2*A–O*, 12*B*, 15*A*)

Material examined

Holotype. New Caledonia: Crouy Reef, AMS C.204232 (1pv).

Paratypes. New Calendonia: Anse Vata, Noumea, AMS C.204233 (1pv). Australia: Queensland: trawled Lady Musgrave Island, in lagoon, QM MO.34149 (4pv).

Other material examined. **New Caledonia**: Anse Vata, Noumea, AMS C.37946 (1pv); Ile Signal, off Noumea, 4 m, reef and sand, AMS C.107219 (1pv); Noumea, AMS C.141440 (2lv). **Australia:** Queensland: dredged by 'Kunara', Saumaurez Reef, KL (1pv).

Description and diagnosis

Shell obovate, solid and thick, glossy, well inflated; umbones raised, prosogyrate; lunule heart-shaped, raised, well delineated by incised line; anterodorsal margin long, rounded terminally; ventral margin widely convex; posterodorsal margin moderately convex, steeply sloping, angulate at its posterior termination; lunule raised, elongated heart-shaped, well delineated by incised line. Sculpture of dense concentric striae, with faint to slightly raised ridges at posterior extremity. Hinge of lv with anterior lateral tooth solid, thick, peg-like; anterior cardinal very thin, separated from median cardinal by narrow V-shaped socket; median cardinal thick, oblique, raised; posterior cardinal free, thin, elongate and oblique; posterior lateral thin, parallel to nymph. Hinge of rv with broad anterior pit, anterior cardinal thick, slightly oblique, median cardinal, moderately thick, peg-like, slightly oblique; posterior cardinal oblique, peg-like; posterior lateral, parallel to nymph. Anterior muscle adductor scars tear-drop shaped, posterior adductor scars ovate. Pallial line wide; pallial sinus diminutive. Colour externally white with irregular, obscure pink and dark to light brown blotches (sometimes extensive), solid tents and occasional short rod-shaped markings, umbones white, lunule white with small pale red–brown spot umbonally; shell internally white. Shell dimensions are given in Table 1.

Distribution and habitat

Known only from Queensland and New Caledonia, dredged in coral reef lagoons.

Remarks

In size, shell thickness and glossy surface texture, *L. macaulayi* most closely resembles *L. castrensis*, with which it occurs sympatrically on the Great Barrier Reef (Lady Musgrave lagoon), Saumarez Reef and New Caledonia. However, the truncate posterior margin, the less ovate valve shape and the irregular, more obscure markings readily and consistently distinguish *L. macaulayi* from *L. castrensis*, even in very juvenile material. *Lioconcha ornata* (Dillwyn), *Lioconcha annettae* Lamprell & Whitehead and *Lioconcha berthaulti* n. sp. also share the same habitat as *L. macaulayi*, but differ from that species in their trigonal shape, lack of posterior margin truncation, smaller size and more complex colour patterns.

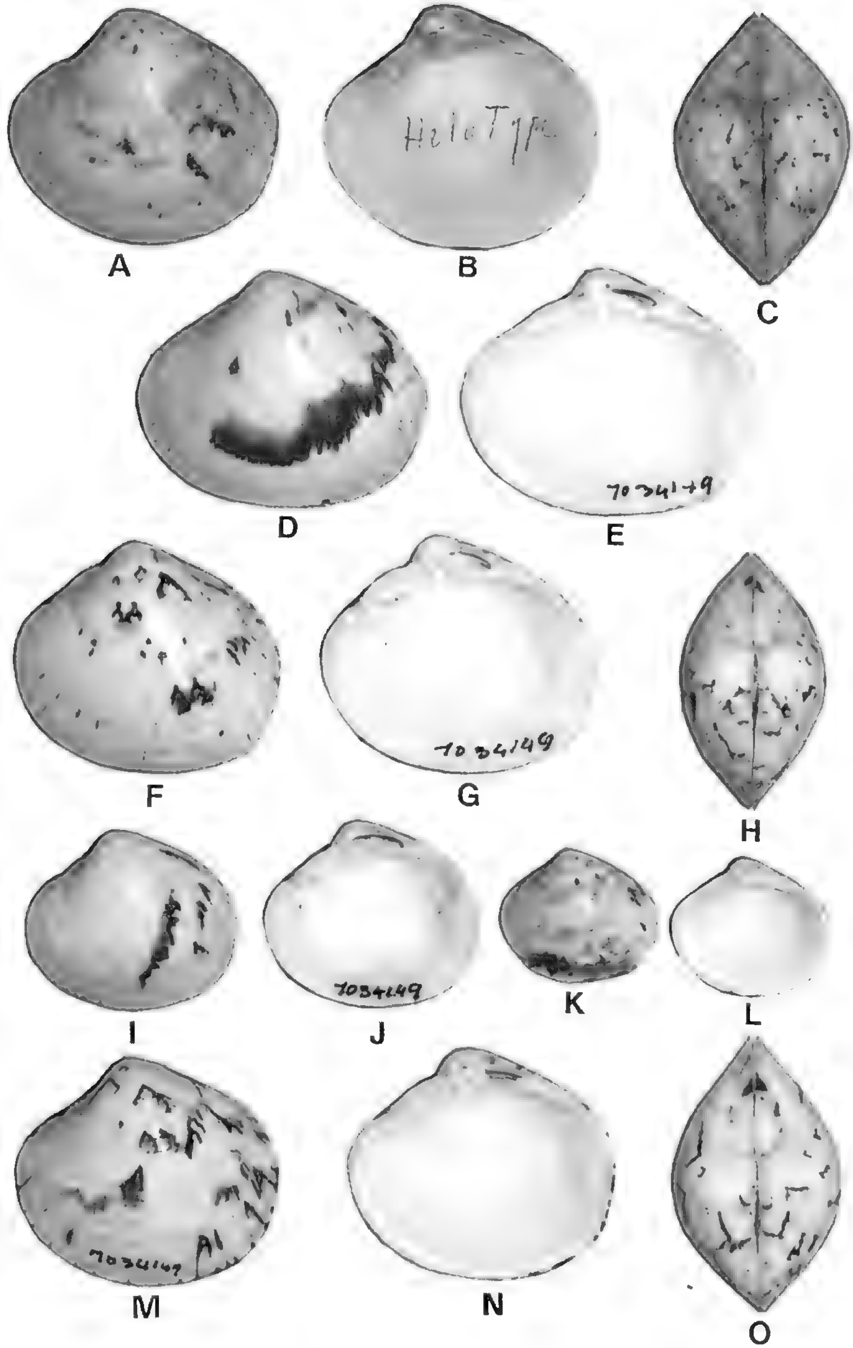

Fig. 2. *Lioconcha macaulayi* n. sp. *A–C*, holotype, Crouy Reef, New Caledonia, AMS C.204232, length 43.5 mm, height 39 mm, width of pv 27.7 mm: *A*, external view lv; *B*, internal view rv; *C*, dorsal view pv. *D–J*, *M–O*, paratypes, trawled Lady Musgrave Island, in lagoon, QM MO.34149: *D*, external view lv; *E*, internal view rv, length 37.5 mm; *F*, external view lv; *G*, internal view rv; *H*, dorsal view pv; length 34.2 mm; *I*, external view lv; *J*, internal view rv, length 29.5 mm; *M*, external view of lv; *N*, internal view rv; *O*, dorsal view pv. *K,L*, juvenile, Anse Vata, Noumea, AMS C.204233, length 20.5 mm: *K*, external view lv; *L*, internal view rv.

Table 1. Shell dimensions of type material of *Lioconcha macaulayi* n. sp.

	Length (mm)	Height (mm)	Width (mm)
Holotype			
AMS C.204232	43.5	39.0	27.7
Paratypes			
AMS C.204233	20.4	18.1	12.1
QM MO.34149 A	47.4	31.6	21.7
B	36.8	32.3	22.1
C	34.3	30.7	19.2
D	29.5	25.8	17.9

Etymology

Named for Dr Geoff Macaulay, in recognition of his generous assistance to the authors through the collecting and for donation of bivalve material used in previous studies.

Lioconcha hieroglyphica (Conrad, 1837)

(Figs 3*A–L*, 12*C*, 15*A*)

Cytherea hieroglyphica Conrad, 1837: 253, pl. 19, fig. 22, (type locality: 'Sandwich Islands in muddy marshes near Pearl R.'), lectotype here selected (ICZN 74.4; designation by means of an illustration or description); Hanley 1844: 100, pl. 15, fig.16; Chenu 1859: pl. 14, fig. 4: Sowerby 1851: sp. 105; Lamy and Fischer-Piette 1937: 274.

Circe hieroglyphica (Conrad). Reeve, 1863: pl. 9.

Lioconcha hieroglyphica (Conrad). Römer, 1864–69 (1866): 46; Kay, 1979: 567, fig. 184*C,D*.

Lioconcha hieroglyphica (Conrad). – Abbott & Dance, 1982: 359, fig. 7 (not of Conrad, 1837) (= *L. castrensis* (Linnaeus)).

Material examined

Hawaii: Kaneohe Bay, Oahu, 21°28N, 157°48′W, 9 m, AMS C.61304 (4pv); AMS C.38791 (3pv); 21°0′N, 157°0′W, AMS C.96968 (2pv, 2lv); Pearl Harbour, Oahu Island, 21°22.5′N, 157°58′W, AMS C. 48240 (1pv, 2rv); AMS C.48240 (3pv); 21°0′N–157°0′W, AMS C.96968 (2pv); Sandwich Island (= Hawaii) AMS C.15084 (2pv); AMS C.47864 (1pv).

Diagnosis

Shell subtrigonal, solid, moderately thick, moderately inflated, smooth to glossy; umbones inflated, elevated, strongly prosogyrate; anterodorsal margin acutely rounded terminally, posteriorly truncate; lunule elongated heart-shaped, raised, well delineated by incised line. Sculpture of fine growth striae, sometimes with faint raised ridges posteriorly. Colour externally white, with dark or tan brown rod-like or angular (hieroglyphic) markings; umbones and lunule white; shell internally white. Shell length to 42 mm.

Distribution and habitat

Known only from Hawaii; Mariana and the Marshall Islands (Kay 1979), in loose coral sand.

Remarks

Lioconcha hieroglyphica has been confused in many collections with the hieroglyphic patterned colour form of *L. castrensis*. Although the type specimen cannot be located, the

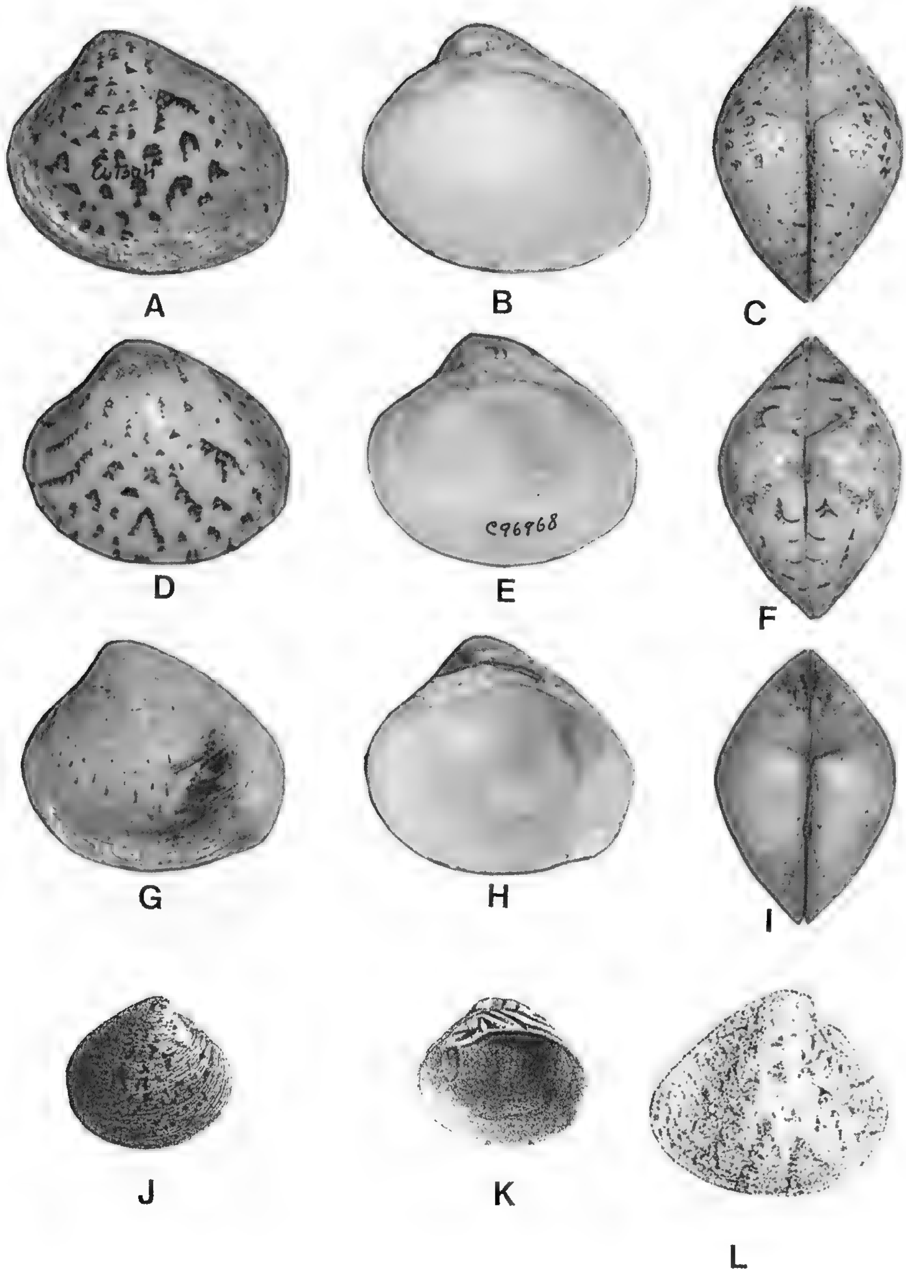

Fig. 3. *Lioconcha hieroglyphica* (Conrad, 1837). *A–C*, Kaneohe Bay, Oahu, length 41.5 mm; AMS C.61304: *A*, external view lv; *B*, internal view rv; *C*, dorsal view pv. *D–F*, Hawaii, length 39 mm; AMS C.96968: *D*, external view lv; *E*, internal view rv; *F*, dorsal view pv. *G–I*, East Loch, Pearl Harbour, Oahu Island, length 38 mm; AMS C.48240: *G*, external view lv; *H*, internal view rv; *I*, dorsal view pv. *J,K*, specimen figured by Chenu (1859) as *Cytherea hieroglyphica* Conrad, 1837: pl. 14, fig. 4: *J*, external view rv; *K*, internal view rv. *L*, Conrad's (1837) original illustration of *Cytherea hieroglyphica* Conrad, 1837: 253, 19, f. 22, external view rv (here selected as lectotype).

description and illustration by Conrad (1837) (see Fig. 3*L* herein; illustration selected as lectotype) and illustrations in Römer (1866) and Kay (1979) are adequate to establish the identity of the species. The Australian Museum collection has eight lots of *L. hieroglyphica* from Hawaii, most specimens of which agree in every aspect with Conrad's description and illustration (Conrad 1837).

Lioconcha tigrina (Lamarck, 1818)

(Figs 4*A–N*, 12*D*, 15*A*)

Cytherea tigrina Lamarck, 1818: 579; no. 34 (refers to Chemnitz, 1782: figs 374, 375), (type locality: 'mer de l'Inde').
Lioconcha tigrina (Lamarck). Prashad, 1932: 220.
Lioconcha (*Lioconcha*) *tigrina* (Lamarck). Lamprell & Whitehead, 1990: 50; Lamprell & Kilburn, 1999*a*: 22, pl. 1, figs 4, 5, 8; Lamprell & Kilburn, 1999*b*: 44.

Material examined

Holotype. MNHG.1084/35, 1pv (Fig. 4*D–F*).
Other material examined. Specimens referred to by Lamarck in Chemnitz Cabinet 'An Chemn. Conch. 6. t. 35. f. 374–375'. Spengler Collection, Copenhagen Museum (Fig. 4*G–L*). **Mauritius**: QM MO.11230 (1pv) (Fig. 4*M–O*); Melvill-Tomlin collection, NMW. Z.1955.158 (1pv). **Mozambique**: see NM material listed by Lamprell and Kilburn (1999*a*).

Diagnosis

Shell solid, moderately thin but very robust, smooth not glossy; triangularly ovate, well inflated; umbones markedly prosogyrate, raised; lunule heart-shaped, flat, weakly outlined by incised line; anterodorsal margin short, moderately sloping; narrowly convex terminally; ventral margin widely rounded; posterodorsal margin straight, steeply sloping, roundly truncate. Sculpture of fine growth striae, supplemented by concentric, flattened ridges at anterior and posterior extremities. Colour externally white with numerous, interconnected, solid triangles of reddish-brown; umbones white, usually with some brown patterning, lunule white or light brown; shell internally white, usually tinged with yellow or orange medially. Shell length to 45 mm.

Distribution and habitat

Western Indian Ocean, in fine littoral sand and mud.

Remarks

This is one of the most poorly understood of all species of *Lioconcha*, due primarily to its close resemblance to *L. castrensis* (another thick, smooth, strongly patterned shell), but also to uncertainties surrounding available type material and its associated locality data ('Oceane Indien'). *Lioconcha tigrina* differs from *L. castrensis* in having posteriorly truncate valves, umbones positioned much closer to the anterior end and a noticeably more compact and better defined lunule. In addition, *L. tigrina* reaches a smaller maximum length (45 mm) than does *L. castrensis* (55 mm). Lamprell and Whitehead (1990) introduced *L. annettae* for a species previously confused with *L. tigrina*. For comparison, they also figured the holotype of *L. tigrina* housed in the Museum d'Histoire Naturelle, Geneva (108/35, no. 34). Although there are some shape and pattern resemblances between *L. tigrina* and *L. annettae*, the closest relationship of the former clearly lies with *L. castrensis* and *L. hieroglyphica*, whereas the latter is associable with the *L. fastigiata* and

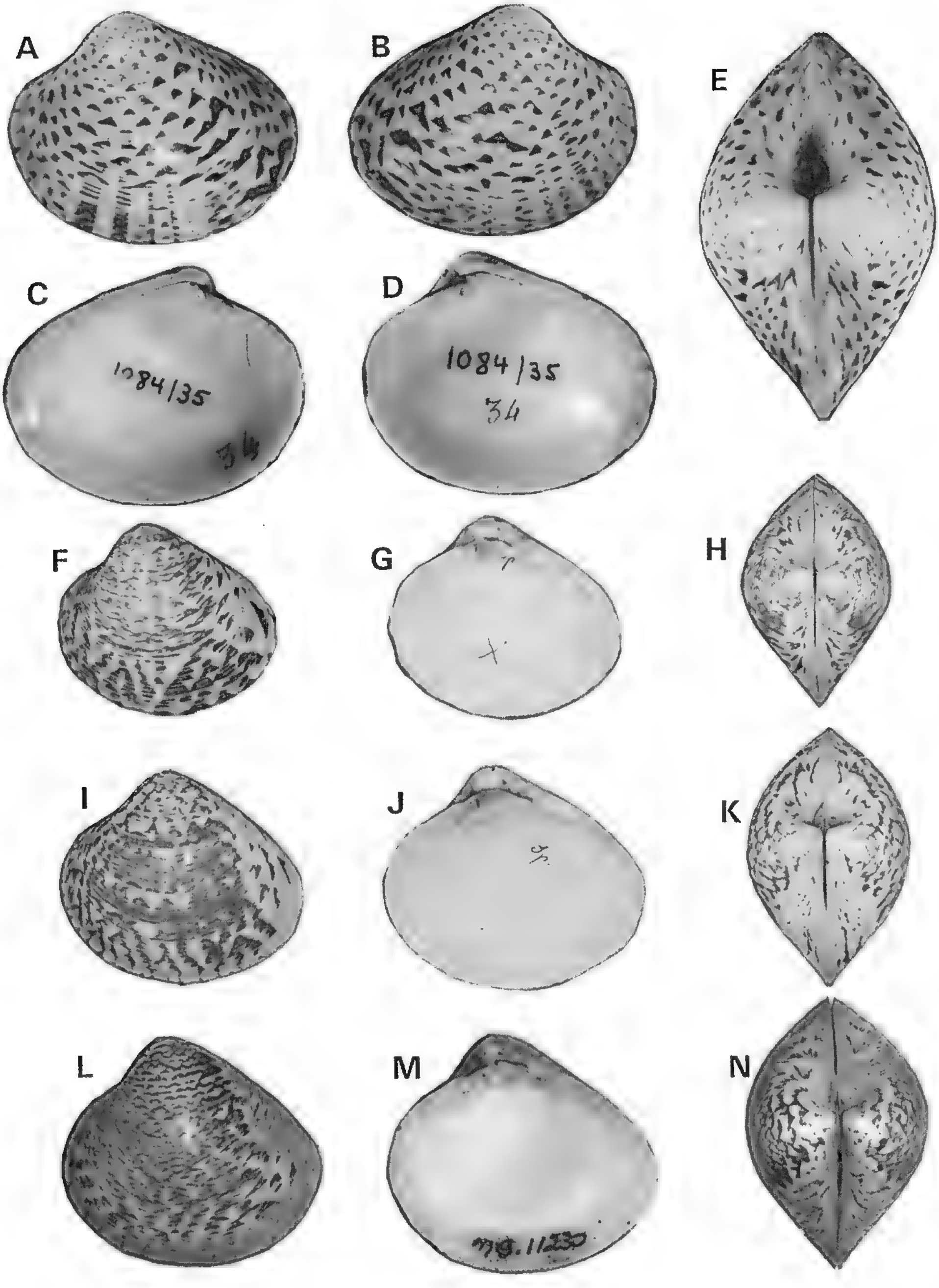

Fig. 4. *Lioconcha tigrina* (Lamarck, 1818). *A–E*, Holotype, 'mer de l'Inde', MNHG.1084/35: *A*, external view lv; *B*, external view rv; *C*, internal view lv; *D*, internal view rv; *E*, dorsal view pv. *F–K*, specimens referred to by Lamarck 'An Chemn. Conch. 6. t. 35. f. 374–375' but having no type status, from Spengler Collection, species 374: *F*, external view lv; *G*, internal view rv; *H*, dorsal view pv; species 375: *I*, external view lv; *J*, internal view rv; *K*, dorsal view pv. *L–N*, Mauritius, 37.9 mm, QM MO.11230: *L*, external view lv; *M*, internal view rv; *N*, dorsal view pv.

L. ornata species complex. During the present study, we were fortunate to have at our disposal a large series of *L. castrensis* from the Philippine Islands, the Great Barrier Reef and New Caledonia for comparison with *L. tigrina*. We also have had the opportunity to examine and photograph type material of *L. tigrina* from the Geneva Museum. We have examined a specimen from the western Indian Ocean (QM MO.11230), which agrees with the type series. Lamprell and Kilburn (1999*b*) examined specimens from northern Mozambique that agree with the holotype and figured both the holotype and a typical specimen. Shell length to 45 mm.

Lioconcha fastigiata (Sowerby, 1851)

(Figs 5*A–J*, 6*I*, 12*E*, 15*B*)

Cytherea fastigiata Sowerby, 1851: 643, (type locality: Sydney, Australia), lectotype (here selected, as Sowerby's (1851) illustration 158, pl.; ICZN 74.4; designation by means of an illustration or description; see Fig. 6*A* herein).
Circe fastigiata (Sowerby). Reeve, 1863: sp. 41.
Lioconcha fastigiata (Sowerby). Römer, 1864–69 (1868); 45, fig. 1*a–c*; Springsteen & Leobrera, 1986: 298, pl. 85 fig. 4.
Lioconcha (*Lioconcha*) *fastigiata* (Sowerby). Habe, 1977: 258; Lamprell & Whitehead, 1992: no. 546.

Material examined

Type material examined. Possible syntypes (presently labelled as 'syntypes', 'Sydney, Australia') BMNH.20000455 (5pv).

Other material examined. **Australia: Western Australia**: One Arm Point, littoral sand, AMNH. 303274 (2pv); Broome, AMS C.141100 (1rv, 1lv); Buccaneer Archipelago, AMS C.42458 (many). **Northern Territory**: Vashon Head, Port Essingon, Coburg Peninsula, AMS C.93083 (2pv); Friday Island, Torres Strait. **Queensland**: AMS C.96956 (2lv); Mapoon, AMS C.14238 (5lv, 1rv); Bowling Green Bay, Townsville, AMNH.303036 (1pv); trawled off Palm Island, AMNH.303315 (8pv); Dingo Beach, AMNH.303037 (1pv); Gloucester Passage, Dingo Beach, AMS C.72153 (4pv); Hayman Island, AMS C.97340 (2pv); Bustard Heads, Port Curtis, AMS C.141411 (1pv); Myora, Stradbroke Island, AMNH.303373 (2pv). **Thursday Island**: Torres Strait, AMS C.141413 (1pv). **Philippine Islands**: (no localised data) QM MO.14448 (in part) (1pv).

Diagnosis

Shell ovate–trigonal to trigonal, moderately thin but strong, smooth to glossy, well inflated, posteriorly somewhat attenuate in large adults; umbones prosogyrate (more so in large adults) and raised; lunule heart-shaped, flat, weakly delineated by incised line; anterodorsal margin short, steeply sloping; narrowly convex terminally; ventral margin widely rounded; posterodorsal margin straight, steeply sloping, narrowly rounded at its extremity. Sculpture of growth striae supplemented by slightly raised ridges at anterior and posterior extremities. Colour externally white with heavy, black, ragged chevron patterns, lunule with prominent purple–black blotch; umbones white, lunule white with large brown–black blotch umbonally; shell internally white, sometimes with cream flesh colour centrally. Shell length to 38 mm.

Distribution and habitat

Western Indian Ocean to the West Pacific, in littoral muddy sand (not known from lagoonal or reef areas).

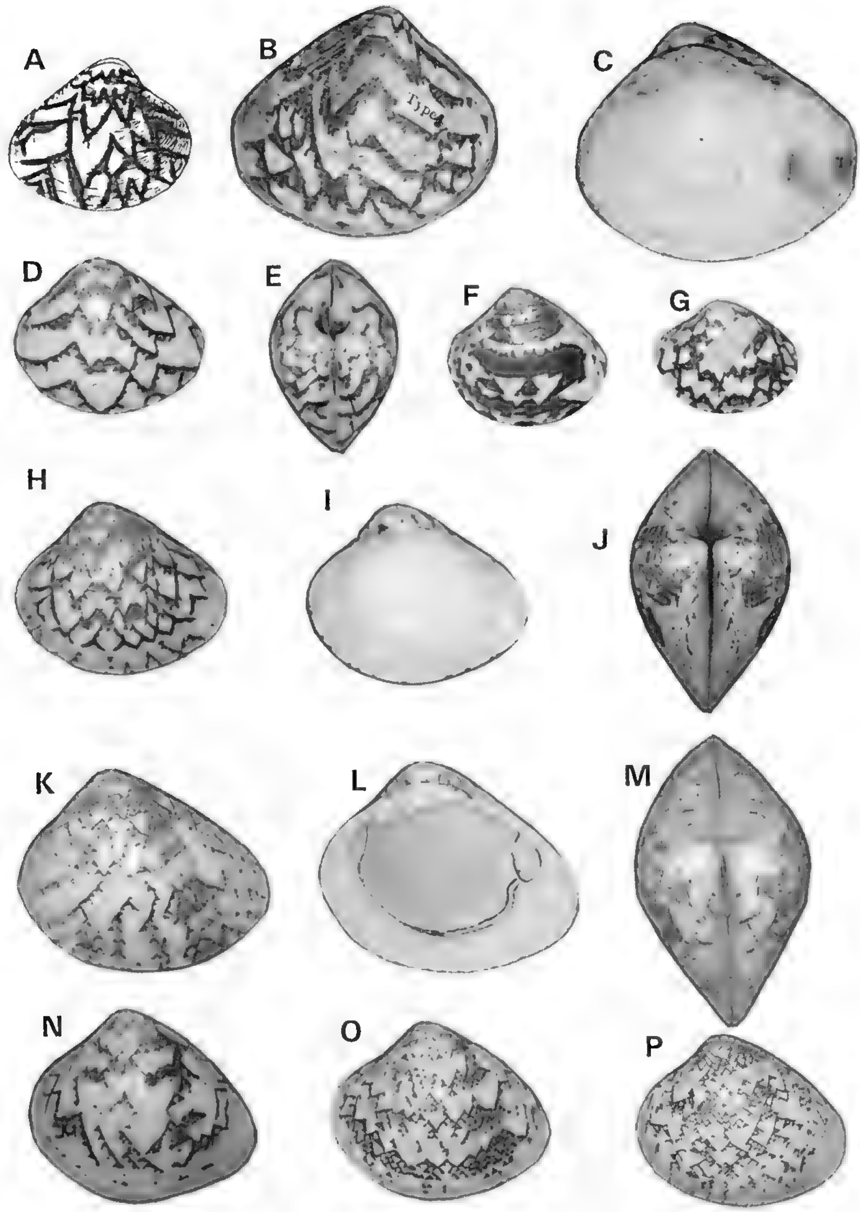

Fig. 5. *A–J, Lioconcha fastigiata* (Sowerby, 1851). *A, Cytherea fastigiata* (fig. 158 of Sowerby (1851), here selected as lectotype) external view rv; *B*, external view rv of largest specimen presently carded as one of the 'syntypes' from Cuming Collection (BMNH.20000455) and marked with the word 'Type' glued to the shell (note: designator unknown; neither this specimen nor other material from lot BMNH. 20000455 match either fig. 158 or 159 of Sowerby (1851); see also Fig. 6*G* herein for reproduction of fig. 159 from Sowerby (1851)); *C*, internal view rv (same specimen as *B*). *D,E*, Palm Island, N Qld, length 33.5 mm: *D*, external view lv; *E*, dorsal view pv, AMNH.303315; *F*, Philippine Islands, QM MO.14448 (in part), length 22 mm, external view lv: *G*, Philippine Islands, QM MO.14448 (in part), length 15 mm, external view lv; *H–J*, Palm Island, N Qld, AMNH.303315, length 37.8 mm: *H*, external view lv; *I*, internal view rv; *J*, dorsal view pv. *K–P, Lioconcha annettae* Lamprell & Whitehead, 1990. *K–M*, Holotype, Swains Reef, QM M0.22852, length 39 mm: *K*, external view lv; *L*, internal view rv; *M*, dorsal view pv; *N*, Lady Musgrave Island, in lagoon, Qld, KL, length 41 mm, external view lv; *O*, Taylor Reef, Qld, KL, 39 mm, external view lv; *P*, Crouy Reef, New Caledonia, KL, length 37.2 mm, external view lv.

Remarks

The five pv from the Natural History Museum (BMNH.20000455) are labelled as 'syntypes'. Although these specimens were from the Cuming collection and the largest specimen has the word 'Type' glued to the shell, none matches either of Sowerby's (1851) illustrations of *C. fastigiata* (his figures 158, 159). There is no indication as to who originally gave the status of syntypes to the material in lot BMNH.20000455 (J. Pickering, personal communication). We have therefore decided to downgrade the status of this material from 'syntypes' to 'possible syntypes' and, in the absence of any definite type material, herein select Sowerby's figure 158 as the lectotype (ICZN 74.4). Sowerby's figure 159 closely resembles *Lioconcha pseudofastigiata* n. sp., based on the external coloration and the attenuate valve shape (see Fig. 6*G* herein), but, in the absence of any illustration of the interior of the shell by Sowerby (or any matching specimen from the Natural History Museum collection), it is impossible to be absolutely certain of the identity of this specimen. Sowerby gives 'Sydney, Australia' as the locality for *L. fastigiata*, but if his figure 159 represents *L. pseudofastigiata* n. sp. (a species presently recorded only from the Philippine Islands), then it would seem highly likely that some, and possibly all, of his material was collected in the Philippine Islands. We know of no records of this species from Sydney or any locality south of Moreton Bay, southern Queensland.

This is a well known and reasonably common species, recorded from several localities throughout the Indo-West Pacific. The colouration of dark brown zigzag flammules over the valves and the dark brown blotch associated with the lunule, combined with the smooth, inflated shell appear to be constant within the species and help to distinguish it from other species of *Lioconcha*. Superficially *L. fastigiata* may be mistaken for *L. castrensis* (which also shows zigzag flammules), but that species always has a thick, rounded shell featuring a heavy hinge line (and teeth) and a strongly raised lunule. Specimens of *L. fastigiata* from the Philippine Islands differ from those from Australia in having more elongate, slightly thinner shells, which exhibit a diffuse brown band internally. The relationship between *L. fastigiata* and *L. annettae* seems to be a very close one, although the former is chiefly a coastal inhabitant, whereas the latter is always found in reef lagoonal localities. It is possible that *L. annettae* may prove to be a localised reef form of *L. fastigiata*, but until the relevant anatomical and/or molecular data become available to test this suggestion, we continue to recognise both as valid taxa. Certain forms of *L. ornata* (in the rather broad sense adopted herein) examined in the present study, especially material from New Caledonia, also suggest a relationship between this species, *L. fastigiata* and *L. annettae*. Again, this requires clarification based on non-conchological characters. Cernohorsky (1972) illustrates a fairly typical specimen of *L. fastigiata* from Caboni Beach, Fiji, and this represents the most easterly confirmed record of this species within the Pacific. Although Kira (1962) records *L. fastigiata* from Japanese waters ('the Amami Islands and southwards', p. 162) his illustrated specimen is clearly identifiable as *L. ornata*.

Lioconcha annettae Lamprell & Whitehead, 1990

(Figs 5*K–P*, 12*F*, 15*C*)

Lioconcha (*Lioconcha*) *annettae* Lamprell & Whitehead, 1990: 49, fig. 4*e–h*; Lamprell & Whitehead, 1992: sp. 545; Lamprell & Stanisic, 1996: 17: 27–48.

Material examined

Holotype. Australia: Queensland: Swain Reef, dredged coral sand, D. and V. Harris, 1986, QM M0.22852 (1pv).

Paratypes. Australia: Queensland: Lady Musgrave Island, coral sand, 3–7 m, dredged, D. and V. Harris, 1986, AMS C.160474 (1pv), WAM.941–89 (1pv).

Other material examined. **Australia: Queensland**: Lady Musgrave Island, in lagoon, AMNH.303126 (4pv); Herald Prong Reef, Swains Reef, AMNH.303163 (6pv); Kelso Reef, dredged 3–7 m coral sand, MV F.57681 (1pv); Taylor Reef; KL (1pv), AMNH.303029; Kelso Reef, AMNH.303025 (1pv); Swains Reef, AMS C.132082; Queens Beach, Bowen, AMS C.75887 (in part); Rudder Reef, off Port Douglas, AMS C.138072 (4pv); Murray Island, Torres Strait, AMS C.138080. **New Caledonia**: Poum Bay, Daomboui Island, 0–3 m, in sand and coral, 20°9′S, 163°59′E, AMS C.356679 (in part) (1pv) (preserved); Anse Vata, Noumea, AMNH.303031–AMNH.303269 (2pv); Baie des Citrous, Noumea, AMNH.303034 (1pv); Crouy Reef, Noumea, AMNH.303030 (1pv). (For further New Caledonian sites, refer to Lamprell and Stanisic (1996).) **Indonesia**: Wai Island, Sorong, NW Irian Jaya, 5–10 m in rubble on coral slope, AMNH.303045 (1pv). **Philippine Islands**: Bohol Island, Tagbilaran, 9°39.000′N, 123°51.000′E, AMS C.371090 (1lv).

Diagnosis

Shell moderately thin but strong, trigonal, smooth to glossy, well inflated, becoming somewhat attenuate posteriorly in large adults; umbones prosogyrate (markedly so in large adults) and raised; lunule elongate heart-shaped to lanceolate, flat, weakly delineated by incised line; anterodorsal margin short, steeply sloping; narrowly convex terminally; ventral margin convex (slightly sinuate in very large adults); posterodorsal margin straight, steeply sloping, narrowly rounded at its extremity. Sculpture of fine, dense, growth striae supplemented by raised concentric ridges ventrally, anteriorly and posteriorly. Colour externally white, with black, chestnut or dark-brown chevron or hieroglyphic patterns and microscopic dots; umbones and lunule white, with purple spots beneath umbones; shell internally white, yellow centrally. Periostracum straw coloured. Shell length to 41 mm.

Distribution and habitat

Western Pacific and Eastern Indian Ocean (Irian Jaya), in coral sand, lagoonal and reef areas.

Remarks

Lamprell and Whitehead (1990) differentiated *L. annettae* from *L. tigrina* and *L. fastigiata* on the basis of valve profile, sculpture and colouration. They further separated *L. annettae* from *L. fastigiata* using habitat preferences (reef for the former, mainland coastal for the latter), maximum shell length and the length of the teeth. Examination of a more extensive series of specimens (including juveniles) than that available to Lamprell and Whitehead suggests that there are no significant differences between the species as regards teeth length or valve profile. Whereas it is true that mature *L. fastigiata* tend to be smaller (generally 25–30 mm in length) than *L. annettae* (generally 30–40 mm in length), we have examined a number of specimens of *L. fastigiata* comparable in size to average *L. annettae*. The differences between *L. annettae* and *L. fastigiata* in habitat preference, adult sculpture and colouration (including lunule colouration) appear to hold, but the basic patterning of the shells is similar and suggestive of a close relationship. As to the precise nature of this connection, whether that of sister species, subspecies or populational variants, nothing can as yet be concluded. Lamprell and Stanisic (1996) recorded *L. annettae* from several subtidal stations off New Caledonia. We can confirm this, but add that several interesting specimens from this region appear to be intermediate between *L. annettae* and *L. ornata*,

suggestive of occasional hybridisation and, as with *L. fastigiata*, also a close relationship. Lamprell and Stanisic (1996) previously indicated that *L. annettae* and *L. ornata* may eventually prove to be conspecific but, based on shell features alone, the closest relationship of *L. annettae* would seem to lie with *L. fastigiata*.

Lioconcha pseudofastigiata n. sp.

(Figs 6*A–H*, 13*A*, 15*B*)

Material examined

Holotype. Philippine Islands: Leyte, littoral sand, AMS C.204480 (1pv).

Paratypes. Philippine Islands: Cebu, Mactan Island, Punta Engano 10°19.000′N, 124°1.000′E ('90–145 m. Tangle nets' (sic)), AMS C.1633076 (7pv, 1lv); 'Philippines', purchased Sowerby and Fulton, Kew, London, QM MO.14448 (4pv).

Description and diagnosis

Shell ovate–trigonal; thin but strong, smooth; anterior end of shell less than one-third of maximum length; medially inflated; umbones raised, markedly prosogyrate; anterodorsal margin short, rounded terminally; ventral margin widely convex; posterodorsal margin almost straight, steeply sloping, narrowly rounded and attenuate terminally; lunule elongate heart-shaped, flat, obscurely delineated by incised line; ligament impressed. Sculpture of concentric striae and well-defined growth pauses, terminating at postero–umbonal ridge. Hinge of lv with anterior lateral tooth thin, peg-like; anterior cardinal very thin, separated from median cardinal by inverted V-shaped socket; median cardinal thick, oblique, joined to anterior lateral at top; posterior cardinal free, thin, elongate and oblique; posterior lateral thin, parallel to nymph. Hinge of rv with broad anterior pit, anterior cardinal thin, slightly oblique, median cardinal, moderately thick, peg-like, slightly oblique; posterior cardinal oblique, long, thin; posterior lateral, parallel to nymph. Anterior muscle adductor scars teardrop shaped, posterior adductor scars subovate. Pallial line thin, well defined; pallial sinus diminutive. Colour: externally white with irregularly arranged, solid tents of brown–black (sometimes fused laterally); umbones and lunule white, with purple spots beneath umbones; umbones white or pale pink; lunule white but with large brown–black blotch; shell internally white, sometimes flesh coloured umbonally, always with very wide, diffuse purple–brown ray or blotch medially (darkest at ventral margin). Shell dimensions are given in Table 2.

Distribution and habitat

Known only from the Philippine Islands, in littoral sand and mud.

Remarks

Lioconcha pseudofastigiata n. sp. occurs sympatrically with *L. ornata*, at least based on locality data for certain material of both species from the Australian Museum (*L. pseudofastigiata*, AMS C.163076; *L. ornata*, AMS C.163075). Depth and collection method information associated with these lots ('In tangle nets, 90–145 m') should probably be disregarded, because the holotype of *L. pseudofastigiata* and all examined material of the closely allied species *L. fastigiata*, *L. annettae* and *L. ornata* are from shallow water (in most cases unknown from depths greater than 10 m; *L. ornata* occasionally recorded from up to 50 m). We have examined *L. fastigiata* from the Philippine Islands, which agree in all

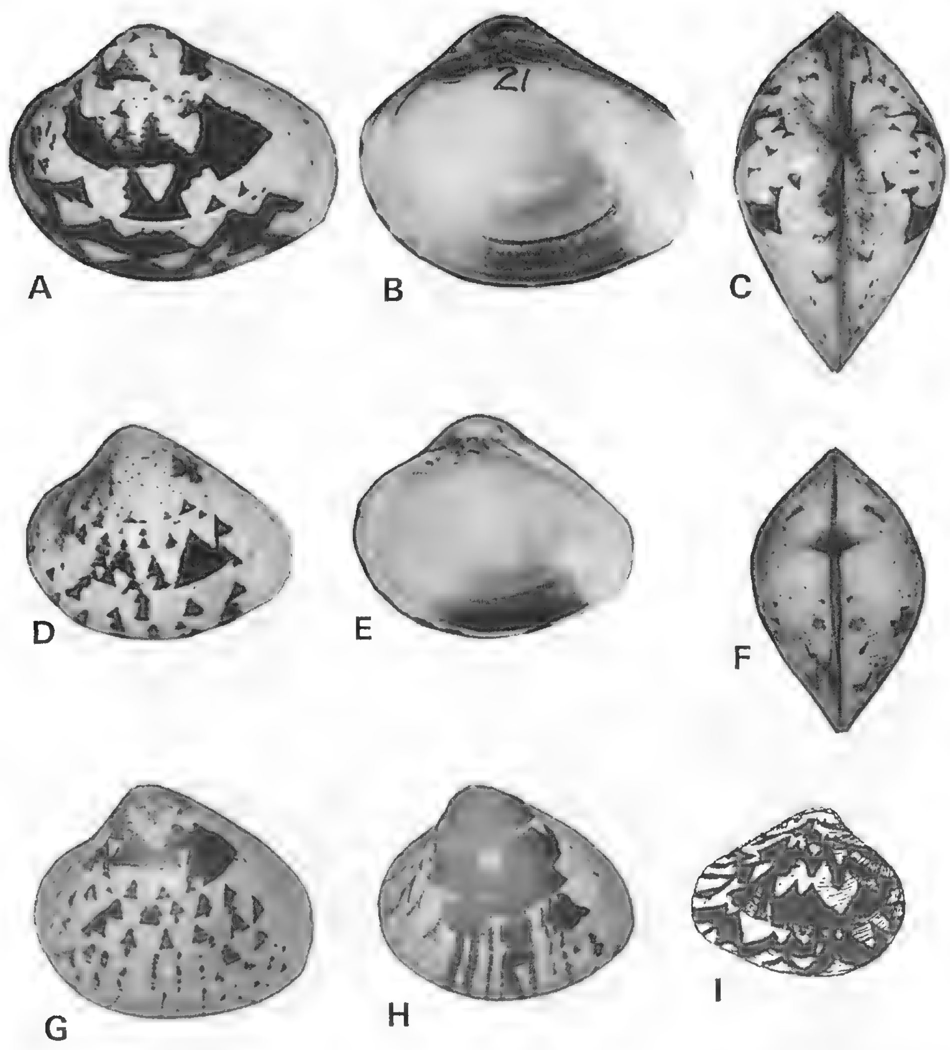

Fig. 6. *A–H*, *Lioconcha pseudofastigiata* n. sp. *A–C*, Holotype, Leyte, littoral sand, Philippines, AMS C.204480, length 34.5 mm: *A*, external view lv; *B*, internal view rv; *C*, dorsal view pv; *D–F*, paratype, Cebu, Mactan Island, Punta Engano 10°19.000′N, 124°1.000′E, AMS C.163076, length 30.8 mm: *D*, external view lv; *E*, internal view rv; *F*, dorsal view pv; *G,H*, Philippine Islands, QM MO.14448, external views lv (length 43.7 and 40 mm, respectively); *I*, *Cytherea fastigiata*, fig. 159 from Sowerby (1851), external view rv; this figure (= strictly, a paralectotype of *Lioconcha fastigiata*) closely resembles shells of *Lioconcha pseudofastigiata* and is probably a representation of that species.

respects with Australian specimens, but we cannot conclude whether *L. fastigiata* and *L. pseudofastigiata* occur sympatrically. Sowerby's (1851) fig. 159 of *C. fastigiata* (an external view of a rv and, strictly, a paralectotype of *L. fastigiata*; see Fig. 6*I* herein) resembles shells of *L. pseudofastigiata* and is probably a representation of this new species (for further comments on Sowerby's material see remarks under *L. fastigiata*). The moderately thin shell, distinctive external pattern of solid tenting and consistent presence of a wide, purple–brown ray or blotch internally all help to distinguish *L. pseudofastigiata* from *L. fastigiata* and *L. annettae*.

Table 2. Shell dimensions of type material of *Lioconcha pseudofastigiata* n. sp.

	Length (mm)	Height (mm)	Width (mm)
Holotype			
AMS C.204480	34.5	27.5	20.5
Paratypes			
AMS C.163076 A	27.7	23.0	17.1
B	31.5	18.9	24.5
C	30.8	24.0	17.5
D	29.0	23.3	17.7
E	27.3	21.5	16.8
F	27.7	22.7	17.3
G	25.5	21.6	16.7
H	24.3	19.7	8.1 (1rv)
QM MO.14448 A	40.0	34.5	25.4
B	43.7	36.9	26.2
C	28.2	24.6	18.5
D	24.8	20.2	13.8

Lioconcha ornata (Dillwyn, 1817)

(Figs 7*A–I*, 13*B,C*, 15*D*)

Venus castrensis var., Röding, 1798: 181, no. 294 (refers to Chemnitz, 1782: figs 380, 381).
Venus ornata Dillwyn, 1817: 184, no. 61 (based on Chemnitz, 1782: figs 380, 381), (type locality: Tranquebar, Mauritius); Wood, 1818: 36, no. 60.
Lioconcha (*Lioconcha*) *ornata* (Dillwyn). Habe, 1977: 258; Oliver, 1992: 185, pl. 40 figs 2; Lamprell & Whitehead, 1992: sp. 544; Lamprell & Stanisic, 1996: 32, fig. 2*e,f*; Lamprell & Kilburn 1999*a*: (neotype designated), 22, pl. 1, figs 9–14; Lamprell & Kilburn 1999*b*: 44.
Lioconcha ornata (Dillwyn). Prashad, 1932: 219.
Lioconcha (*Lioconcha*) *ornata* (Lamarck) (sic). Abbott & Dance, 1982: 359.
Cytherea picta Lamarck, 1818: 579, no. 33 (refers to Chemnitz, 1782: figs 373, 376–381) (in part), (type locality: Indian Ocean); Lamy & Fischer-Piette, 1937: 274.
Lioconcha picta (Lamarck). Lamy, 1930: 135.

Material examined

Venus ornata. Syntypes lost; neotype (designated by Lamprell and Kilburn (1999*a*)) Mauritius, Spengler collection (figs 9–11) ZMUC (1pv; see discussion below).

Other material examined. **Australia: Queensland**: trawled between Palm and Curacoa Islands, AMNH.303472 (7pv); trawled lagoon, Little Trunk Reef, AMNH.303471 (4pv); Slashers Reef no. 1, in lagoon, 10 m, AMNH.303284 (6pv); Lizard Island, AMNH.303283 (1pv). **Papua New Guinea**: 5–6 m, in sand around coral shoal, between Kranket Island and Madang, 5°12′S, 145°50′E, AMS C.356678 (5pv) (preserved); northern end Madang, 5°12′S, 145°51′E, AMS C.358000 (5 rv, 4lv). New Britain: Duke of York Island, AMS C.68234 (1pv). **Indonesia**: Kalimantan, 14 km N of mouth of Mahakan R., KL (1lv). **Solomon Islands**: Honiaro beach, AMNH.303374 (1pv). **New Caledonia**: Secteur de Koumac, 10–16 m, AMNH.303406–AMNH.303409 (4pv); Anse Vata, AMNH.303285 (1pv); Noumea, AMS C.86251 (many) (full New Caledonia locality data is provided Lamprell and Stanisic (1996)). **New Hebrides**: AMNH.303279 (1pv). Fiji: Nadi Bay, 34.5 m, AMS C.67589 (many). **Philippine Islands**: Tabangao, Batangas Prov, Luzon Island, AMS C.104739 (1pv); Sulu Sea, Cuyo Islands, AMS C.2228 (1rv, 1lv); Luzon Island, entrance to Manila Bay, Corregidor Island, AMS C.138086 (1rv); Luzon Island, Bauang, Perez Beach, AMS C.141441 (1rv, 1lv); Palawan Island, N Hondo Bay, Tanabag Beach, AMS C.371091 (1rv). **Mozambique–Northern Zululand** (for full localities refer Lamprell and Kilburn (1999*a*), all NM material). **Mauritius**: AMS C.96966 (1pv). **Red Sea**: Dissal Island, off Massana, AMS, no number (3pv); NE of Safaga Town, among coral and sand, NMW. Z.1997.021.100 (1pv). **Israel**: Eilat, KL (6pv).

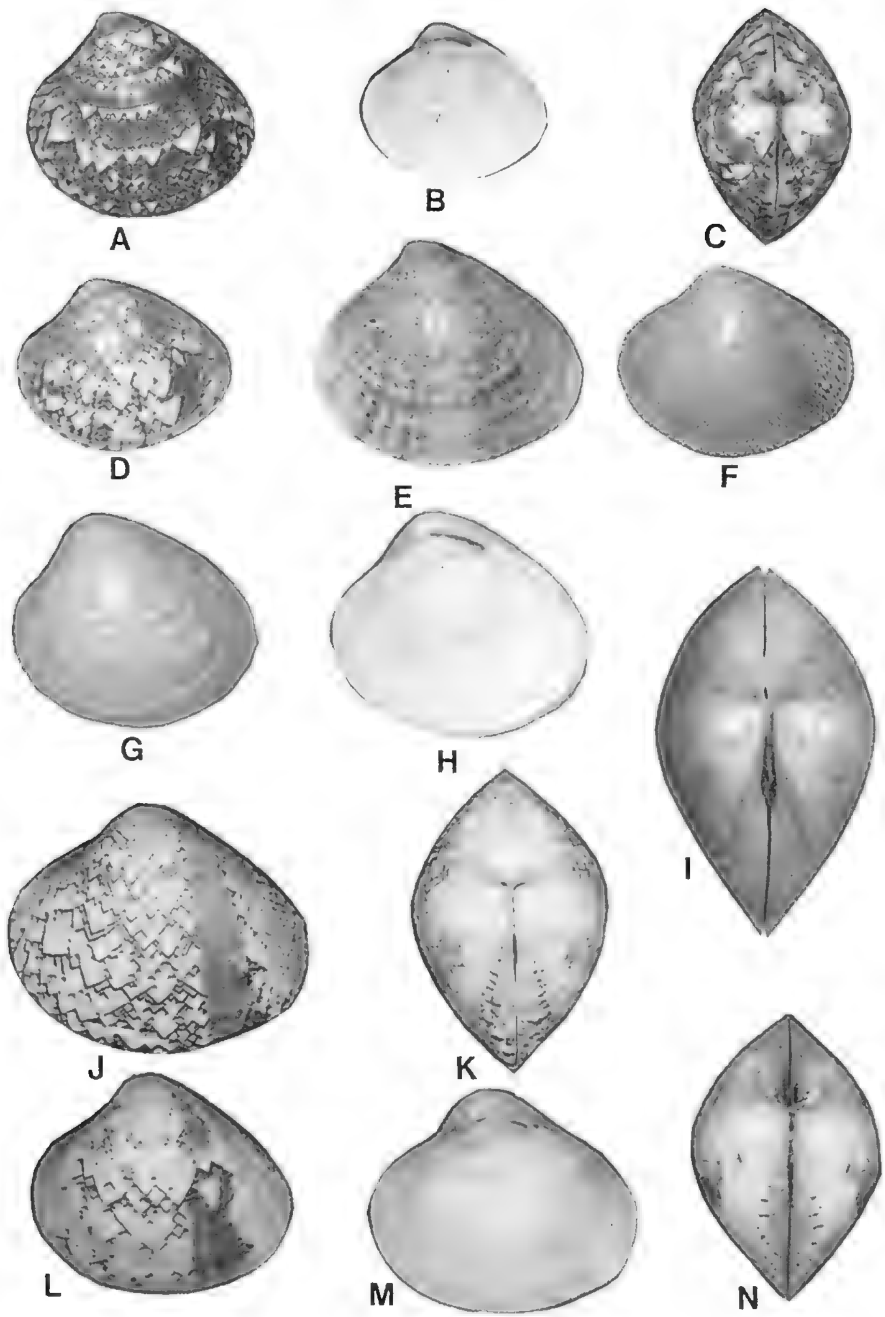

Fig. 7. *A–I*, *Lioconcha ornata* (Dillwyn, 1817). *A–C*, Neotype, Spengler Collection, length 26.2 mm: *A*, external view lv; *B*, internal view rv; *C*, dorsal view pv; *D*, specimen from Spengler Collection, external view lv; *E*, Palm Island, N Qld, QM MO.34141, 38 mm, external view lv; *F*, Honiara, Solomon Islands, AMNH.303038, length 32 mm, external view lv; *G–I*, Slasher's Reef no. 1, AMNH.303284, length 43.3 mm: *G*, external view lv; *H*, internal view rv; *I*, dorsal view pv. *J–N*, *Lioconcha berthaulti* n. sp. *J,K*, Holotype, Broadhurst Reef, E of Townsville, AMS C.136078, length 31.7 mm: *J*, external view lv; *K*, dorsal view pv; *L–N*, paratype QM MO.65962, 18°76.7′S, 147°89.9′E, N Qld, length 30 mm: *L*, external view lv; *M*, internal view rv; *N*, dorsal view pv.

Diagnosis

Shell ovate–trigonal to trigonal, solid, smooth to glossy; umbones raised, slightly prosogyrate but markedly so in large adults; lunule elongate heart-shaped to lanceolate, flat, faintly delineated by incised line; anterodorsal margin short, widely rounded terminally; ventral margin widely convex; posterodorsal margin slightly convex, steeply sloping, narrowly rounded at termination. Sculpture of obscure concentric striae, well defined at anterior and posterior margins and stronger growth pauses. Colour externally white with brown blotches forming a dense network of fine chevron markings (tent shaped) over entire surface; umbones white, lunule white often with light-brown staining near umbones; shell internally white usually with yellow or pale orange medially. Dimensions of neotype: length 28.3 mm, height 26.2 mm, width of pv 18.5 mm. Shell length to 48 mm.

Distribution and habitat

Indo-West Pacific (including Japan (Habe, 1977)) in coral sand or loose sand and rubble, littoral to about 50 m.

Remarks

Lamprell and Kilburn (1999*a*) established a neotype for this species from material in the Spengler Collection. This material is representative of what we may term 'typical' *L. ornata*. During the course of the present study, we have examined several specimens, especially from the south-western Pacific, which indicate to us that *L. ornata* (as broadly interpreted herein) either represents a complex of species, subspecies or geographic variants or, as recently suggested by Lamprell and Stanisic (1996), is simply an extremely variable species with the ability to generate a number of distinctive colour and/or morphological forms at any one locality. As indicated elsewhere in this paper, occasional specimens of *L. ornata* may show shape and/or pattern similarities to *L. fastigiata* and *L. annettae* and, by so doing, somewhat blur the boundaries between these three taxa. Unfortunately, examination of the hinge teeth from an extensive range of material has not yielded any characters to help separate these three species, leaving colour pattern, valve shape and sculpture as the only useful means of discrimination. Specimens from Israel often show a patch of purple internally and are trigonal, even in very juvenile specimens. A very attractive form from the Solomons and New Guinea exhibits minute rows of spots, which merge into fine zigzag markings near the dorsal edge. Specimens from the outer region of the Great Barrier Reef are large (45–48 mm), heavy, trigonal and exhibit minute tents in their patterning. The frequent occurrence of intermediates between several of the 'forms' suggests that they are all merely variants within a single species. However, it is hoped that future molecular and/or detailed anatomical work will assist in determining whether some of the more distinctive forms here grouped under the name *L. ornata* deserve to be recognised taxonomically.

Lioconcha berthaulti n. sp.

(Figs 7*J–N*, 13*D*, 15*E*)

Material examined

Holotype. Australia: Queensland: 18°57′S, 147°44′E, Broadhurst Reef, off Townsville, subtidal, AMS C.138078 (1pv).

Paratypes. Australia: Queensland: Station 048, 18°76.7′S, 147°89.9′E, 47 m, QM MO.65962 (1pv); Lizard Island, NTM P.12500 (2pv, 1rv (juvenile)).

Other material examined. **Australia: Queensland**: Little Broadhurst Reef, May 1993, Rowse Collection (1pv); Station 031, 18°82.9′S, 147°59.6′E, 53 m, KL (1pv); Lizard Island (1rv), Wistari Reef, Heron Island, Willan Collection (2rv, 3lv). **New Caledonia**: Grand Recif Sud, Stn 552, 22°54′S, 166°55′E, 38 m, MNHN (1rv); Secteur de Belep, Station 1088, 19°46′S, 163°58′E, 23 m, MNHN (1lv, 1pv).

Description and diagnosis

Shell ovate–trigonal; thin but strong, smooth but not glossy; anterior end of shell less than one-third of maximum length; medially inflated; umbones raised, markedly prosogyrate, especially in large adults; anterodorsal margin short, narrowly rounded terminally; ventral margin widely convex; posterodorsal margin almost straight, steeply sloping, narrowly rounded and attenuate terminally; lunule elongate heart-shaped, flat, obscurely delineated by incised line; ligament impressed. Sculpture of concentric striae and well-defined growth pauses, terminating at postero-umbonal ridge. Hinge of lv with anterior lateral tooth thin, peg-like; anterior cardinal very thin, separated from median cardinal by inverted V-shaped socket; median cardinal thick, oblique, joined to anterior lateral at top; posterior cardinal free, thin, elongate and oblique; posterior lateral thin, parallel to nymph. Hinge of rv with broad anterior pit, anterior cardinal thin, slightly oblique, median cardinal, moderately thick, peg-like, slightly oblique; posterior cardinal oblique, long, thin; posterior lateral, parallel to nymph. Anterior muscle adductor scars tear-drop shaped, posterior adductor scars ovate. Pallial line wide; pallial sinus diminutive. Colour externally white with a dense network of fine chevron markings (tenting) over entire surface, one broad, orange ray extends from umbones to posteroventral margin, one broad ray composed of fine pale pink dots lies between orange ray and escutcheon; umbones white, lunule usually speckled with brown; shell internally white or very pale flesh colour. Shell dimensions are given in Table 3.

Distribution and habitat

Known only from Queensland and New Caledonia, in coral reef and sand areas to 53 m.

Remarks

This small to medium sized species approaches most closely *L. annettae* and *L. ornata* in size and shape, but can be easily separated from both of these by its more inflated, thinner shell and very distinctive broad orange colour ray posteriorly and narrower hinge plate. In addition, the anterior lateral tooth is smaller and less projecting than in either *L. annettae* or *L. ornata* and, in mature specimens, of *L. berthaulti*, the posterodorsal margin is abruptly

Table 3. Shell dimensions of type material of *Lioconcha berthaulti* n. sp.

	Length (mm)	Height (mm)	Width (mm)
Holotype			
AMS C.38078	31.7	27.0	20.5
Paratypes			
QM MO.65962	30.0	25.5	20.5
NTMP.12500 A	30.0	25.4	20.02
B	19.4	16.2	12.2
C	23.8	20.5	9.2 (rv)
D	14.8	12.8	5.3 (rv)

truncate. Mature *L. annettae* and *L. ornata* also normally reach a considerably larger size than *L. berthaulti*. *Lioconcha castrensis* may, in its very juvenile state, show similar tenting of the pattern, but the shell is always more ovate and thicker than *L. berthaulti*, with a much more robust hinge plate and teething. This species has been taken from the same dredge sample as *L. annettae* at one Queensland locality (a complete and fresh juvenile pv, Station 031 18°82.9′S, 147°59.6′E) and as a single dead left valve in the same dredge sample off New Caledonia (Secteur de Belep, Station 1088), together with fresh pv of *L. ornata* and both fresh and single-valve juveniles of *L. castrensis*. Presumably *L. berthaulti* lives sympatrically with one or more other species of *Lioconcha*. The broad orange band may be very faded in dead shells and it is interesting to note that very occasional specimens of *L. ornata* may show a narrow orange band posteriorly, suggesting at least the possibility of some interspecific hybridisation. *Lioconcha berthaulti* appears to be a moderately rare subtidal species, with a known distribution from the Great Barrier Reef off Townsville to New Caledonia.

Etymology

Named for Mr Claude Berthault in recognition of his generous assistance to the authors through the collecting and donation of several lots of *Lioconcha* used in the present study.

Lioconcha sowerbyi (Deshayes, 1853)

Figs 8*A–N*, 13*E*, 15*E*

Cytherea hebraea Sowerby, 1851: sp. 100, figs 143, 144, 148 (not of Lamarck).
Circe sowerbyi Deshayes, 1853: p. 2, sp.7; Reeve, 1863; sp. 29, figs *a,b*.
Lioconcha sowerbyi (Deshayes). Römer, 1864–69 (1866): 46.

Material examined

Lectotype. Figured specimen 148 in Sowerby (1851); figured specimen 29a in Reeve (1863); ex Cuming collection; BMNH.19991518/1 (1pv); here designated (ICZN 74.4; designation by means of an illustration or description); (type locality: Manila, Philippine Islands). Measurements of lectotype: length 31.4 mm, height 27.4 mm, width of paired valves 20.2 mm.

Paralectotypes. Figured specimen 29b in Reeve (1863), BMNH.19991518/2 (1pv); not figured; ex Cuming collection, BMNH.19991518/3 (1pv).

Possible syntypes. Ex Cuming collection, not figured, BMNH.19991519/1 (1pv); ex Cuming collection, not figured, BMNH.19991519/2 (1pv).

Other material examined. **Philippine Islands**: Manilla Bay, QM MO.14505 (2pv).

Diagnosis

Shell ovate–trigonal, moderately thin but strong, smooth but not glossy, moderately inflated; anterior and posterior margins convex and attenuate, ventral margin evenly convex; umbones only slightly projecting, slightly prosogyrate; lunule heart-shaped, flat, weakly delineated by incised line. Sculpture of fine growth striae supplemented by dense, concentric, raised ridges and stronger, irregular growth pauses. Colour externally white with red–brown pattern of small zigzags, often intersected by radial rays of white or red–brown; umbones white, lunule white or brownish; shell internally white, with varying expanses of dark red–brown medially. Shell length to 41.2 mm.

Distribution and habitat

Known only from the Philippine Islands in sandy mud.

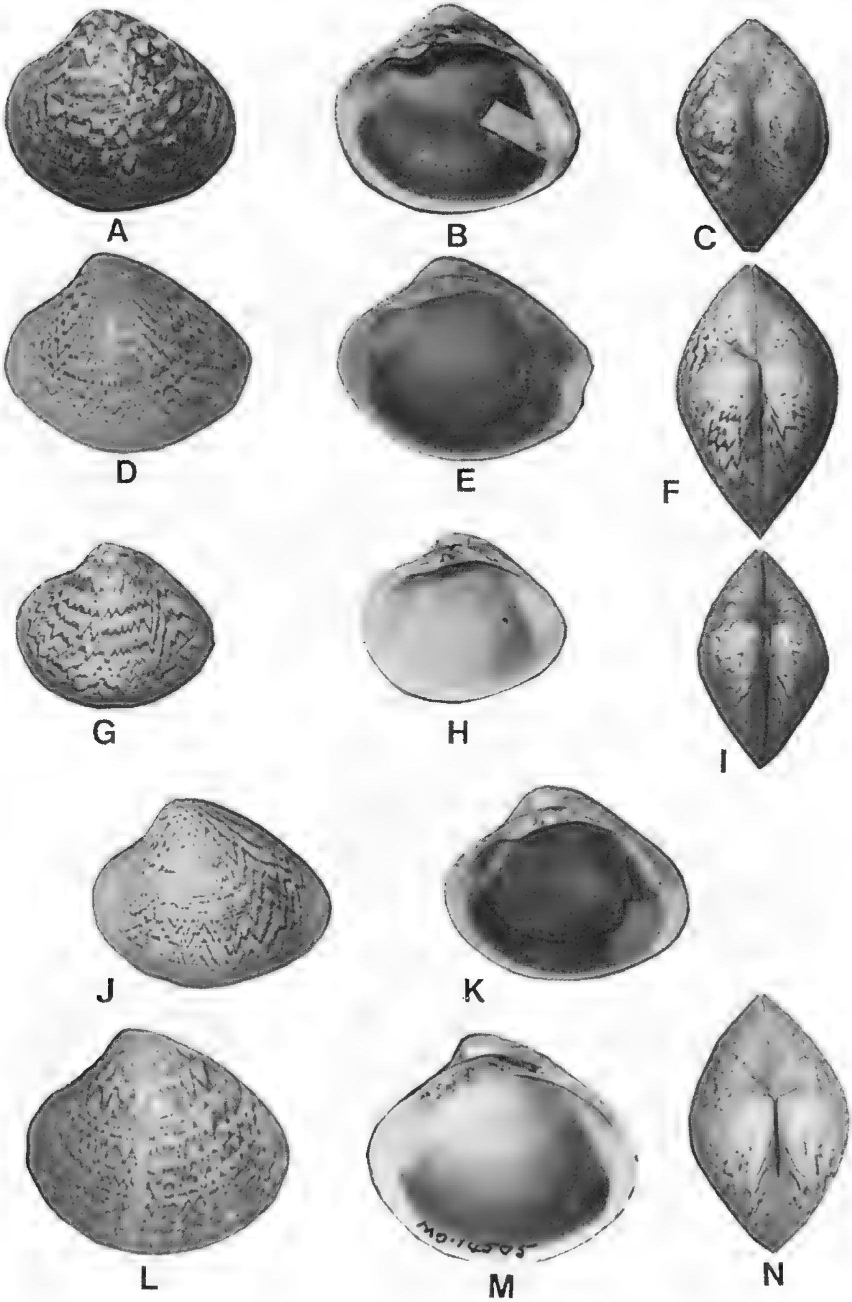

Fig. 8. *Lioconcha sowerbyi* (Deshayes, 1853). *A–C*, Lectotype, here designated BMNH.19991518/1, length 31.4 mm, height 27.4 mm, width of pv 20.2 mm: *A*, external view lv; *B*, internal view rv; *C*, dorsal view pv. *D–F*, Fig. spec. 29b (Reeve 1863), BMNH.19991518/2, length 41 mm: *D*, external view lv; *E*, internal view rv; *F*, dorsal view pv. *G–I*, Probable syntype, ex Cuming collection, Manila, Philippine Islands, BMNH.19991519/1, 31.5 mm: *G*, external view lv; *H*, internal view rv; *I*, dorsal view pv. *J,K*, ex Cuming collection, BMNH.19991518/3, 39.5 mm: *J*, external view lv; *K*, internal view rv. *L–N*, Manilla Bay, Philippine Islands, QM MO.14505, length 32 mm: *L*, external view lv; *M*, internal view rv; *N*, dorsal view pv.

Remarks

Although *L. sowerbyi* closely resembles *L. schioettei* n. sp. in shape and colour, it lacks the sinuate posteroventral margin of that species and differs in internal colouration (brown staining medially in *L. sowerbyi*, mauve–purple staining posteriorly in *L. schioettei*). *Lioconcha sowerbyi* and *L. schioettei* show a remarkable, but convergent, resemblance in colour pattern to *Pitar* (*Pitarina*) *abbreviata* (Krauss) (fine red–brown zigzags interrupted by growth pauses and by rays of white extending from the umbones). The presence of a well-developed pallial sinus in *P. abbreviata* clearly shows that this species is not a member of the genus *Lioconcha*. *Lioconcha trimaculata* differs from *L. sowerbyi* and *L. schioettei* in its smaller size, more regular and better developed concentric ridges, external colouration (emphasising rays, lacking zigzags), purple-brown lunule and escutcheon and in the internal colouration (typically muscle scars with brown staining).

The syntypes of *C. hebraea* Sowerby, 1851 (not of Lamarck, 1818 = *Circe sowerbyi* Deshayes, 1853) have been located in the BMNH. The specimen illustrated by Sowerby (1851; figure 148, BMNH.9991518/1) has been isolated and is here designated as the lectotype in order to fix the type. Sowerby's figured specimens 143 and 144 from the Gubba collection have not been located. Other specimens from the Cuming collection and associated with the lectotype (BMNH.19991518/1–2) are here designated as paralectotypes, whereas two other specimens (BMNH.19991519/1–2), also from the Cuming collection, are possible syntypes.

Lioconcha polita (Röding, 1798)

Figs 9*A–J*, 13*F*, 15*E*

Venus polita Röding, 1798: 181, (type locality not given (= Nicobar Islands, Chemnitz, 1782: 371–372).
Cytherea sulcatina Lamarck, 1818: 568, (type locality: 'l'Océan indien' nr. 29), (refers to Chemnitz, 1782: 371–372); Lamy & Fischer-Piette, 1937: 273.
Circe (*Lioconcha*) *sulcatina* (Lamarck). Lynge, 1909: 233 (early references).
Lioconcha sulcatina (Lamarck). Melvill & Sykes, 1898: 48; Lamy, 1930: 135; Oliver, 1992: 186, pl. 40, fig. 3.
Lioconcha polita (Röding). Prashad, 1932: 218.
Lioconcha (*Lioconcha*) *polita* (Röding). Lamprell & Kilburn 1999*a*: 21, pl. 1, figs 1–3 (= *L. schioetti* n.sp. herein, see p. 126).

Material examined

Type material examined. The specimen illustrated by Chemnitz (1782; figs 371, 372; Nicobar Island, Spengler collection ZMUC), used as the basis for Röding's (1798) description of *L. polita*, has been isolated and is here figured and designated as the lectotype in order to fix the type. Dimensions of lectotype: length 41.5 mm, height 35 mm, width of paired valves 27 mm.

Other material examined. Specimen from MNHN, marked on associated label '*Cytherea sulcatina* Lamarck var 2, Individual named by Lamarck. No status'.

Diagnosis

Shell solid, trigonal, smooth to glossy, moderately inflated, posteriorly attenuated; umbones strongly prosogyrate; lunule heart-shaped, flat, delineated by well-incised line. Sculpture of flattened concentric ridges posteriorly and growth pauses. Colour externally white with dark, radial, brown or orange rays, often interacting with rays composed of zigzag or chevron patterns; umbones white or light brown, lunule brownish; shell internally white, sometimes brown or orange medially. Shell length to 41.5 mm.

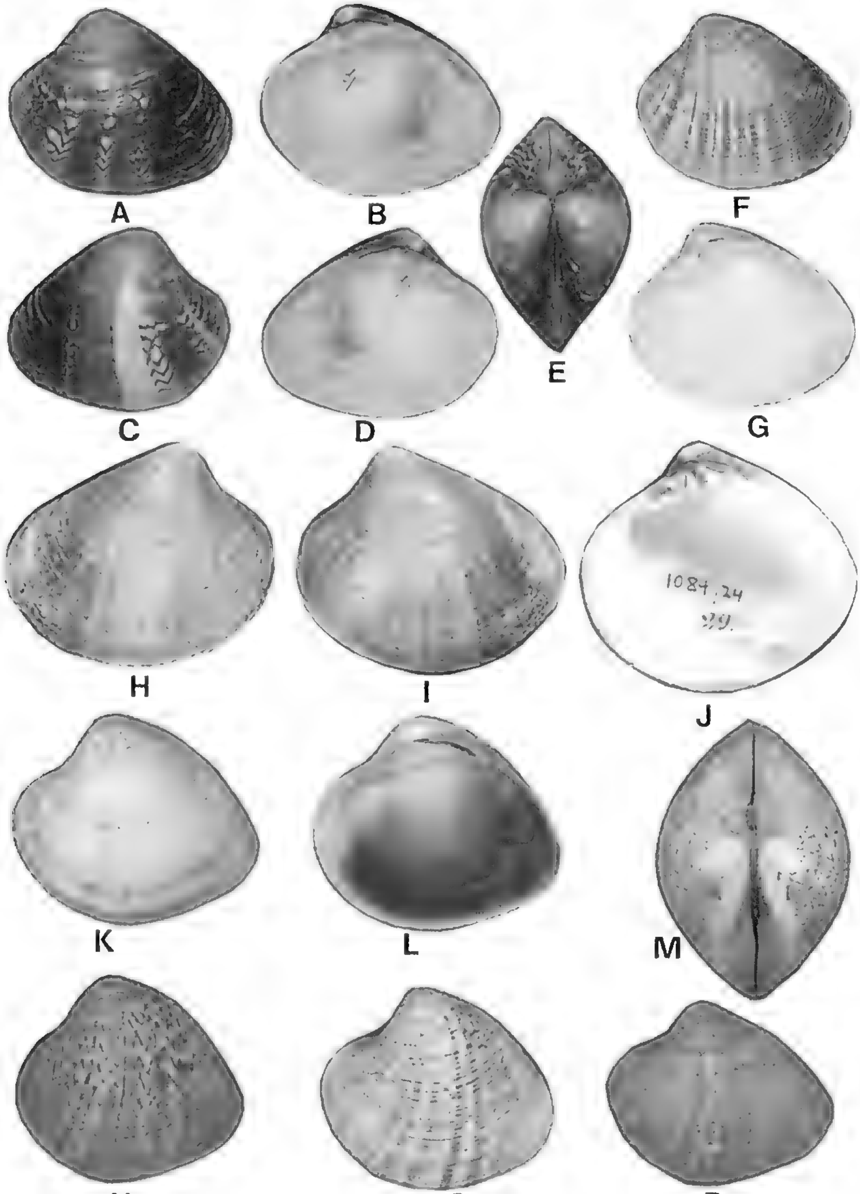

Fig. 9. *A–J*, *Lioconcha polita* (Röding, 1798). *A–E*, Specimen illustrated by Chemnitz (1782), figs 371 and 372, Nicobar Island, Spengler collection ZMUC, length 41.5 mm, height 35 mm, width of pv 27 mm: *A*, external view lv; *B*, internal view rv; *C*, external view rv; *D*, internal view lv; *E*, dorsal view pv; *F,G*, specimen from MNHN, marked *Cytherea sulcatina* Lamarck var 2, individual named by Lamarck, no status, length 40 mm, height 33 mm, width of pv 25 mm: *F*, external view lv; *G*, internal view rv; *H–J*, *Cytherea sulcatina* Lamarck, 1818, holotype MHNG.1084/24, length 42.2 mm, height 39 mm: *H*, external view rv; *I*, external view lv; *J*, internal view rv. *K–P*, *Lioconcha schioettei* n. sp. *K–M*, Holotype, Taylor Reef, north Queensland, AMS C.204296, dredged 10 m, height 35 mm, length 42 mm, width of pv 28 mm: *K*, external view lv; *L*, internal view rv; *M*, dorsal view pv; *N*, 20°35′S, 164°12′E, New Caledonia, AMNH.303408, 14–15 m, length 39 mm, external view lv; *O,P*, Palm Passage off Palm Island, AMNH.303412, 10–15 m: *O*, external view lv, length 35.5 mm; *P*, external view lv, length 39.5 mm.

Distribution and habitat

Northern Indian Ocean, littoral areas, in sandy mud.

Remarks

Lioconcha polita can best be compared with *L. sowerbyi*, but the strong groove surrounding the lunule, greater inflation, broad radial colour bands and internally orange or light brown centrally (weak lunule groove, moderate inflation, thin zigzag patterns and deep brown internal colour in *L. sowerbyi*) distinguish the two species. Compared with *L. annettae*, which is also attenuated posteriorly, the broad external radial colour bands, internal orange or light brown colour (sparse tent patterns and yellow internal colour in *L. annettae*) separate the species. The lectotype of *L. polita* is an interesting specimen in that the right and left valves show marked differences in colour patterns, this caused some authors (Lamprell and Whitehead 1992; Lamprell and Stanisic 1996; Lamprell and Kilburn 1999*a*, 1999*b*) to deal with the two Chemnitz (1782) figures (371 and 372) as two separate species. Examination of the specimen from the ZMUC and the Lamarck specimen from the MNHN also show this colour variation; however, the specimen MHNG.1084–24 marked '*Cytherea sulcatina* Lamarck, 1818 holotype' does not. Figure 4*J*, showing the internal rv of MHNG.1084–24, indicates a less elongate shell, but this is due to visual distortion created by the camera angle.

Lioconcha schioettei n. sp.

(Figs 9*K–P*, 13*G*, 16*A*)

Lioconcha (*Lioconcha*) *polita* (Röding). Lamprell & Whitehead, 1992: sp. 547; Lamprell & Kilburn, 1999*a*: 21; Lamprell & Kilburn, 1999*b*: 44 (not Röding, 1798).

Material examined

Holotype. Taylor Reef, north Queensland, dredged 10 m, 1995, AMS C204296 (1pv).

Paratypes. Queensland: 19°02.7′S, 147°62.2′E, 52 m, AMS C.204297 (47pv); trawled off Loadstone Reef, 30 m, QM MO.66997 (2pv).

Other material examined. **Australia: Queensland**: 14°40′S, 145°28′E, on surface of fine, clean sand, offshore from 'Chinaman's Ridge', Watson's Bay, NW coast of Lizard Island, 16 m, NTM P.000975 (1pv, 1lv); 14°40′S, 145°28′E, on fine, clean sand with siphonaceous algae, offshore from 'Chinaman's Ridge', Watson's Bay, NW coast of Lizard Island, 20 m, NTM P.000976 (1rv); Palm Passage off Palm Island, 10–15 m, AMNH.303412 (2pv, 1rv). **New Britain**: Duke of York Island, AMS C.68247 (in part) (1pv). **New Caledonia**: 20°35′S, 164°12′E, 14–15 m, AMNH.303408 (2pv); Noumea (further material listed by Lamprell and Stanisic (1996) under '*Lioconcha* (*Lioconcha*) *polita*'), AMS C.141449 (1pv). **Philippine Islands**: 12°0.000′N, 122°0.000′E, 1935; NMW. Z.1955.158 (9pv) Melville-Tomlin Collection, AMS C.141450 (3pv). **East Timor**: 08°20′S, 125°21′E, in beach drift, Tibar Beach, near Dili, NTM P.000963 (1rv). **Vanuatu** (New Hebrides): Port Vila, AMS C.141448 (3rv, 1lv). **Madagascar**: Nosey-Be, AMNH.303411 (1pv)-AMS C.88985 (1pv). **Tanzania**: Kunduchi Beach, Dar es Salaam, AMS C.124788 (in part) (1rv). **Sri Lanka**: AMS C.107978 (1rv). **Mozambique**: (see Lamprell and Kilburn (1999*a*) for a listing of material and locality data, under '*Lioconcha* (*Lioconcha*) *polita*'). Shell dimensions are given in Table 4.

Description and diagnosis

Shell ovate–trigonal, moderately thin but strong, well inflated, chalky to smooth; umbones raised, slightly to moderately prosogyrate (more so in large adults); anterodorsal margin short, narrowly rounded terminally; anterior margin widely rounded; ventral margin widely convex, slightly but still conspicuously sinuate posteriorly; posterodorsal margin widely

rounded, steeply sloping, narrowly rounded and attenuate terminally; with well-defined postero-umbonal furrow; lunule heart-shaped, flat, obscurely delineated by incised line. Sculpture of fine growth striae supplemented by numerous, slightly raised, concentric ridges, especially over ventral half of valves, and also of well-defined, but irregular, growth pauses. Hinge of lv with anterior lateral tooth thin, peg-like; anterior cardinal separated from median cardinal by inverted V-shaped socket; median cardinal thick, oblique; posterior cardinal free, moderately thin, elongate and oblique; posterior lateral thin, parallel to nymph. Hinge of rv with broad anterior pit, anterior cardinal thin, oblique, short; median cardinal, moderately thick, peg-like; posterior cardinal thick, bifid, oblique; posterior lateral, parallel to nymph. Anterior muscle adductor scars tear-drop shaped, posterior adductor scars ovate. Pallial line wide; pallial sinus diminutive. Colour: externally cream to red–brown with white and red–brown radial rays and diffuse red–brown zigzag markings (the latter stronger umbonally becoming obscure medially); umbones white, lunule light brown or diffuse mauve; shell internally white to yellow, typically stained with mauve posteriorly (mauve staining sometimes extending to median region of valves but often absent in juvenile specimens). Shell dimensions are given in Table 4.

Distribution and habitat

Indo-West Pacific, in clean sand and rubble to 52 m.

Remarks

Examination of several specimens of *L. schioettei* n. sp. from Madagascar, Papua New Guinea, northern Queensland and New Caledonia reveal that *L. schioettei* is reasonably constant in its distinctive valve shape (slightly but consistently sinuate on the ventroposterior margin) and in its colour pattern of intersecting, broken rays and small, somewhat diffuse, zigzag lines. However, the degree of development of the concentric ridges is quite variable, with many specimens observed by us exhibiting pronounced sculpture and others showing very subdued development of the ridges. *Lioconcha sowerbyi* is very similar to *L. schioettei* in shape, surface sculpture and aspects of the external colouration (e.g. also exhibiting fine zigzags of red–brown interrupted by growth pauses and white rays from the umbones) but differs from that species in not having a sinuate posteroventral margin and in being stained brown internally (*v.* mauve posteriorly in *L. schioettei*). *Lioconcha trimaculata* Lamarck, 1818 shows some resemblance to *L. schioettei* in shell shape, but has more extensive patches of brown colouration externally (not containing fine zigzag lines) and a brown to purple–brown dorsal margin. Internally, *L.*

Table 4. Shell dimensions of type material of *Lioconcha schioettei* n. sp.

	Length (mm)	Height (mm)	Width (mm)
Holotype			
AMS C.204296	42.1	35.9	27.5
Paratypes			
AMS C.204297 A	31.7	28.8	20.0
B	30.2	26.6	19.5
C	25.8	21.1	16.3
D	18.6	15.7	11.5
QM MO.66992 A	34.8	30.5	22.2
B	27.8	24.0	18.0

trimaculata typically exhibits a patch of light brown on both the anterior and posterior margins (including the adductor scars), whereas, in *L. schioettei*, purple staining is usually confined to a broad band posteriorly (but not in the region of the anterior adductor scar).

Etymology

Named for Mr Tom Schiotte in recognition of his difficult work in isolating the bivalve species from the Spengler and Moltke collections housed in the ZMUC and figured by Chemnitz (1782).

Lioconcha trimaculata (Lamarck, 1818)

(Figs 10*A–F*, 14*A*, 16*A*)

Cytherea trimaculata Lamarck, 1818: 571, sp. 41; Sowerby, 1851: sp. 102; Lamy & Fischer-Piette, 1937: 273.
Circe trimaculata (Lamarck). Reeve, 1863: pl. 8, sp. 33.
Lioconcha sphragitis Römer, 1868: 162, pl. 43 fig. 3 (*syn. sensu* Hidalgo, 1903: 221), (type locality unknown).
Lioconcha trimaculata (Lamarck). Römer, 1868: 166, pl. 46, fig. 2; Melvill & Sykes, 1898: 172; Habe, 1977: 259; Springsteen & Leobrera, 1986: 304, pl. 86 fig. 18.
Circe (*Lioconcha*) *trimaculata* (Lamarck). Lynge, 1909: 233 (References).
Lioconcha (*Lioconcha*) *trimaculata* (Lamarck). Lamprell & Kilburn, 1999*b*: 45 (Discussion and References).

Material examined

Andaman Islands: Port Blair area, 1858–71, E Man, NMV F.8441 (2 pv, 1rv). **Philippine Islands**: AMNH.303252 (1pv). **New Caledonia**: Nea-Magenta, MNHN, ECOTROPE Expedition. Station (lot 84) (1 pv (juvenile)), littoral collected.

Diagnosis

Shell solid but not thick, ovate, smooth but not glossy, moderately inflated; anterodorsal margin extended anteriorly; posterodorsal margin rounded or slighty attenuate, posteroventral margin showing slight flexure in adults; umbones prosogyrate, more so in adults; lunule flat, heart-shaped, delineated by weakly incised line. Sculpture of fine growth striae supplemented by numerous, fine, concentric, raised ridges over most of valve surface, becoming definable as ribs in ventral half of valve and stronger, irregular growth pauses. Colour externally white, with variously developed rays of brown; lunule and dorsal margin purple or purple–brown; shell internally white or pale peach, usually with light brown associated with adductor. Shell length to 28.5 mm.

Distribution and habitat

Western Pacific, in littoral sand.

Remarks

Lioconcha trimaculata shows similarities to several other *Lioconcha* species, including *L. philippinarum* (Hanley), *L. gordoni* (E. A. Smith), *L. dautzenbergi* (Prashad), *L. schioettei* n. sp. and *L. sowerbyi*. *Lioconcha trimaculata* shares with *L. philippinarum*, *L. gordoni* and *L. dautzenbergi* a purple–brown, clearly incised lunule and a purple–brown escutcheon and predominance of rays in the external colouration. It differs from these three species in lacking the highly glossed surface, in having a much finer ridge sculpture and in

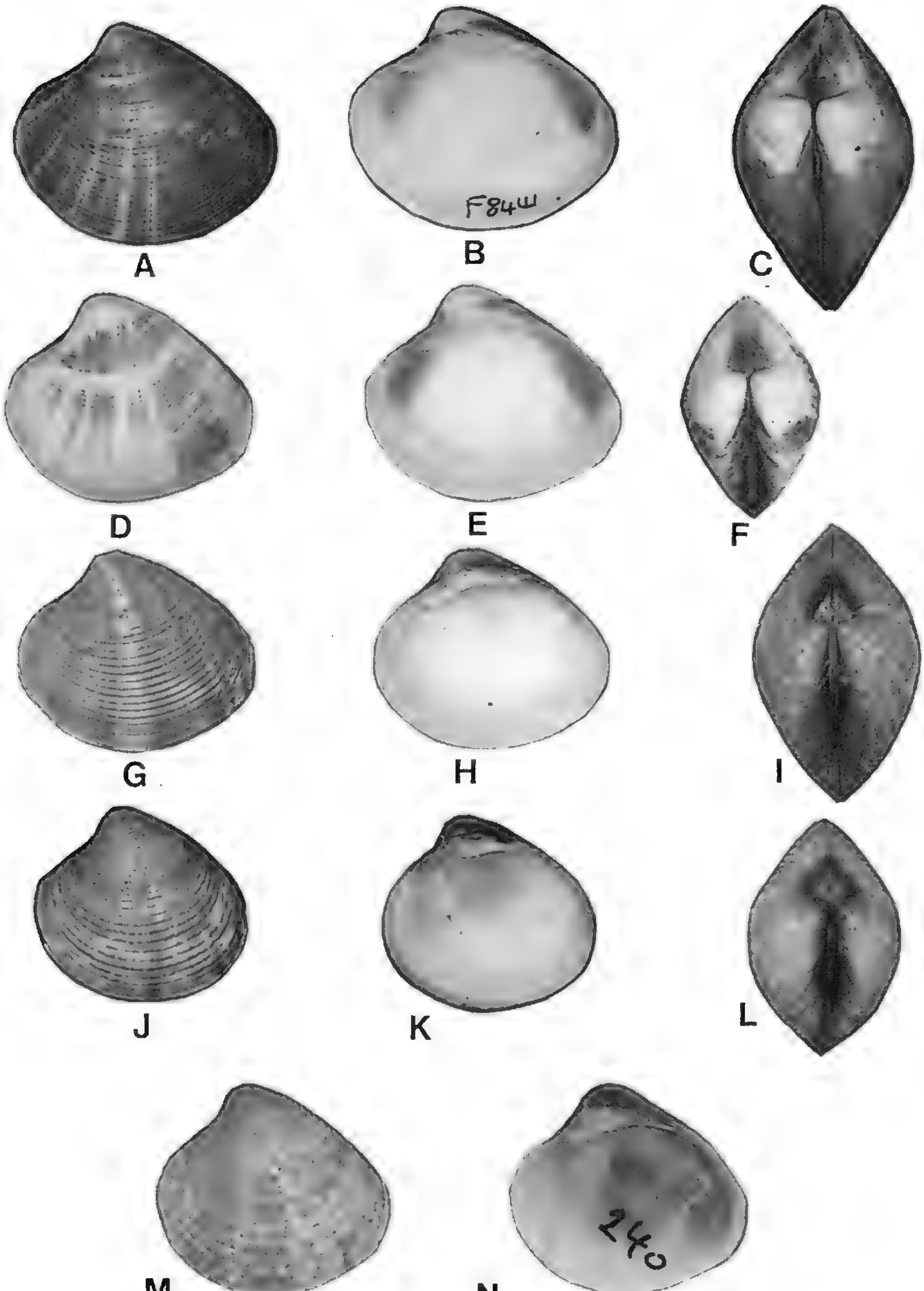

Fig. 10. *A–F, Lioconcha trimaculata* (Lamarck, 1818). *A–C*, Philippine Islands, NMV F.8441: *A*, external view lv; *B*, internal rv; *C*, dorsal view pv; *D–F*, Philippine Islands, KL, length 27.6 mm: *D*, external view lv; *E*, internal view rv; *F*, dorsal view pv. *G–L, Lioconcha philippinarum* (Hanley, 1844). *G–I*, New Guinea, AMNH.303252, 24.5 mm: *G*, external view lv; *H*, internal view rv; *I*, dorsal view pv; *J–L*, New Guinea, P. Pecker coll.: *J*, external view lv; *K*, internal rv; *L*, dorsal view pv. *M,N, Lioconcha dautzenbergi* (Prashad, 1932), holotype, ZMA.3.32.112, length 15.9 mm: *M*, external view lv; *N*, internal view rv.

the positioning of internal staining of the valves (typically anterior and posterior staining in *L. trimaculata v.* subumbonal staining in *L. philippinarum* and *L. gordoni* and median–posterior staining in *L. dautzenbergi*). *Lioconcha trimaculata* shares with *L. sowerbyi* and *L. schioettei* the fine concentric ridge sculpture (although better developed and more regular in *L. trimaculata*), but differs from both these species in external colouration (predominantly rays in *L. trimaculata v.* fine zigzags in *L. sowerbyi* and *L. schioettei*), lunule and escutcheon colouration (purple–brown in *L. trimaculata v.* tan, patterned or white in *L. sowerbyi* and *L. schioettei*) and internal colouration typically anterior and posterior blotches in *L. trimaculata v.* median–posterior mauve staining in *L. schioettei*, median brown staining in *L. sowerbyi*). Lamprell and Kilburn (1999*b*) confirmed the occurrence of this rare species in the Andaman Islands and we can here substantiate Lynge's (1909) New Caledonian record based on our examination of a recently collected juvenile from the Ecotrope Expedition (L'institut Francais de Recherche Scientifique pour le Développement en Coopération), this specimen exhibiting a completely white interior but otherwise agreeing with typical *L. trimaculata*.

Lioconcha philippinarum (Hanley, 1844)

(Figs 10*G–L*, 14*B*, 16*B*)

Cytherea philippinarum Hanley, 1844: 110, (type locality: Philippine Islands); Hanley, 1844: pl. 15. fig. 36; Deshayes, 1863: 12.
Cytherea mendance Philippi, 1851: 72.
Cytherea (*Dione*) *philippinarum* (Hanley). Smith, 1885: 141.
Hysteroconcha (?*Lamelliconcha*) *philippinarum* (Hanley). Prashad, 1932: 217 (References), pl. 6, figs 7–10.
Lioconcha (*Sulcilioconcha*) *philippinarum* (Hanley). Habe, 1951; Lamprell & Stanisic, 1996: 35; Lamprell & Kilburn 1999*b*: 45.
Callista amirantium Melvill, 1909: 132, pl. 4, fig. 12, (type locality: Amirantes Is., 61.2 m, among Polyzoa and shell rubble).

Material examined

Lectotype. *Cytherea philippinarum* Hanley, 1844, H. Harvey Coll., ex Hanley, designated by Lamprell and Kilburn (1999*b*): 45, BMNH.1912.6.18.20.

Paralectotypes. BMNH.1966346/1–7; *Callista amirantium* lectotype designated by Lamprell and Kilburn (1999*b*) three paralectotypes from same lot, BMNH.1910.3.17.14.17.

Other material examined. **Australia:** Murray Island, Torres Strait, AMS C.36345 (1pv); Arafura Sea, 115 m, AMS C.358022 (1rv); Lindeman Island, AMS C.358023 (1lv). **Papua New Guinea**: (ex P. Pecker, no localised data), AMNH.303252 (4pv). **New Britain**: Duke of York Island, AMS C.68244 (in part) (1pv). **Philippine Islands**: AMS C.34910 (2pv). **New Caledonia**: Baie de St Vincent (Lagon: stn 186) (1lv) Secteur de Canala (Lagon: stn 703) (1pv) 40 m; Grand Recif Mengalia (Lagon: stn 839) (2pv, 1lv) 37 m; (stn 849) (1pv, 1lv, 1rv) 41 m; Secteur des Belep (Lagon: stn 1213) (1pv, 1rv) 32 m (MNHN, ORSTOM Expeditions). **Andaman Island**: AMS C.34486 (3pv). **Réunion**: Cap la Houssaye (1lv) 8–17 m, 1984, NM K.4548 (1lv); Saint Paul Bay; 3–30 m, J. Drivas, NM K.2780 (3pv, 14lv, 14rv). **Mauritius**: Off Black R., 24–30 m, NM K.7547 (1pv).

Diagnosis

Shell robust but not thick, elongate–ovate, glossy, moderately inflated; anterior margin rounded; posterior margin rounded, becoming slighty attenuate and truncate in large adults, ventral margin rounded; umbones markedly prosogyrate, more so in adults; lunule heart-shaped, flat, well delineated by incised line. Sculpture of fine growth striae dominated by many coarse, concentric raised ridges developed as rounded ribs; interstices

approximately equal in width to ribs. Colour externally flesh to light brown, with several rays of darker brown and sometimes underlying broad zigzags; lunule and dorsal margin purple-brown; shell internally white with mauve-brown staining subumbonally (staining dominating in small juveniles). Shell length to 27.7 mm.

Distribution and habitat

Indo-West Pacific, in sand and rubble, to 115 m.

Remarks

This is a very distinctive species that is easily differentiated from other heavily ridged *Lioconcha* by a combination of a glossy, flesh to light brown shell (featuring darker brown rays) and a comparatively large adult size. Habe (1951) used this species as the type of his subgenus *Sulcilioconcha* but, as discussed later in the present account, his defining features are inadequate. Habe's reference to a 'purplish' shell appears to apply more so to the inside colouration of the valves rather than the overall external colouration (excepting the lunule area). However, we have not examined Japanese material of *L. philippinarum* and it is possible that geographic variation in external colouration may occur in this species. Although not mentioned by Lamprell and Kilburn (1999*b*), the lectotype of *L. philippinarum* (selected by them) also shows broad, fine zigzag markings. In most specimens examined herein, only faint traces of zigzags could be discerned, largely due to the predominance of brown rays in the colour pattern. On external appearance, *L. philippinarum* is possibly more likely to be confused with certain other heavily ridged venerids, such as various *Callista* species, but these taxa all have a deep, well-developed pallial sinus. The closest relatives to *L. philippinarum* within the genus *Lioconcha* appear to be *L. gordoni* and *L. dautzenbergi*, which, likewise, have glossy shells and exhibit a well delineated lunule tinged with purple–brown (however, in *L. gordoni*, colour is limited to the periphery of the lunule). These species differ from each other in external colour patterns and degree of rib development, irrespective of the size of the individual. In addition, neither *L. gordoni* nor *L. dautzenbergi* reaches the maximum size attained by *L. philippinarum*. *Lioconcha trimaculata* also exhibits a purple–brown lunule, but has a decidedly non-glossy surface and a tendency to show slight sinuation of the posteroventral margin. Lamprell and Kilburn (1999*b*) have recently confirmed Deshayes' (1863) record of this species from Réunion in their survey of venerids from the South African and Mozambiquan region. Lamprell and Kilburn (1999*b*) also note that all specimens from the syntype series of *C. amirantium* are paler than typical Philippine Islands shells, but agree in all other characters.

Lioconcha dautzenbergi (Prashad, 1932)

(Figs 10*M–N*, 14*C*, 16*B*)

Hysteroconcha (?*Lamelliconcha*) *dautzenbergi* Prashad, 1932: 217, pl. 6, figs 11–12, (type locality: Siboga station 240, Banda Sea).
Lioconcha (*Sulcilioconcha*) *dautzenbergi* Prashad. Habe, 1977: 259.

Material examined

Holotype. *Hysteroconcha dautzenbergi* (ZMA 3.32.112).

Diagnosis

Shell robust; ovate–trigonal, glossy; lunule heart-shaped, flat, well delineated by an incised line. Sculpture of fine growth striae largely obscured by wide, rounded concentric ridges

developed as ribs; interstices very narrow compared with width of ribs. Colour externally white-tan, with brown chevron pattern intersected with wide tan rays; umbones, lunule and dorsal margin purple-brown; shell internally white, mauve-purple medially, brown posteriorly. Shell length to 15.8 mm.

Distribution and habitat

Known only from the type locality Siboga stn 240, Banda Sea, habitat unknown (dredged at anchorage in sand).

Remarks

Lioconcha dautzenbergi is a small, distinctive, little known species that is differentiated from other concentrically ridged *Lioconcha* by the fewer stronger concentric ridges, developed as ribs, and very narrow rib interstices. The colouration and shape of the lunule are similar to *L. philippinarum* and, indeed, *L. dautzenbergi* could potentially be confused with that glossy surface species. However, *L. philippinarum* only occasionally exhibits the zigzag lines observed in *L. dautzenbergi*, reaches a larger size and has much narrower, more widely spaced ridges. *Lioconcha gordoni* is similar in size and surface gloss to *L. dautzenbergi*, but the ribs are much narrower, the external colour pattern features zigzags only (no rays of colour), the mauve-purple internal staining is limited to the median portion of the valve and the lunule is primarily white with only a faint tinge of purple peripherally.

Lioconcha melharteae Lamprell & Stanisic, 1996

(Figs 11*A–C*, 14*D*, 16*C*)

Lioconcha (*Sulcilioconcha*) *melharteae* Lamprell & Stanisic, 1996: 35, (type locality: New Caledonia, Grand Recif Sud (Lagon) stn 361, 22°36′S, 167°02′E, 78 m).

Material examined

Holotype. New Caledonia: Grand Recif Sud (Lagon: (1pv) stn 361, 22°36′S, 167°02′E, 29 Nov 1984, 78 m, MNHN.

Paratypes. New Caledonia: Grand Recif Sud (1pv, 3lv, 1rv) stn 370, 22°38′S, 167°06′E, 30 Nov 1984, 127 m; Lagon: (2pv, 2rv) stn 397, 22°39′S, 167°11′E, 23 Jan 1985, 125 m; (1pv, 1lv, 1rv) stn 429, 22°40′S, 167°15′E, 25 Jan 1985, 95 m); Sud Nouvelle-Caledonie (Lagon SMIB: (6pv, 2rv) stn DW81, 22°38′S, 167°35′E, 9 Sep 1989, 110 m); Lagon Nord (Lagon: (1pv) stn 484, 19°00′S, 163°35′E, 2 Mar 1985, 35 m; (5pv) stn 517, 19°09′S, 163°35′E, 5 Mar 1985, 42 m; (1pv) stn 522, 19°08′S, 168°38′E, 5 Mar 1985, 42 m, MNHN; (Lagon: Stn 361, 22°36′S, 167°02′E, 29 Nov 1984, 78 m, AM C.305574 (3pv).

Other material examined. Other New Caledonian (ORSTOM) material is listed by Lamprell and Stanisic (1996), but note that some of these specimens now form the type series for *L. caledonesis* Harte & Lamprell, 1999.

Diagnosis

Shell thin but strong, ovate–trigonal, smooth but not glossy, lunule heart-shaped, outlined by deeply incised line. Sculpture of dense (approximately 80) raised, concentric, rounded ridges developed as fine ribs, which become wrinkled at the anterior and posterior extremities. Colour externally translucent white, with orange ray extending from umbones to posteroventral margin; dorsal margin and lunule also orange; umbones white; internally glossy white with blue-white growth pauses showing through shell surface. Shell length to 21 mm.

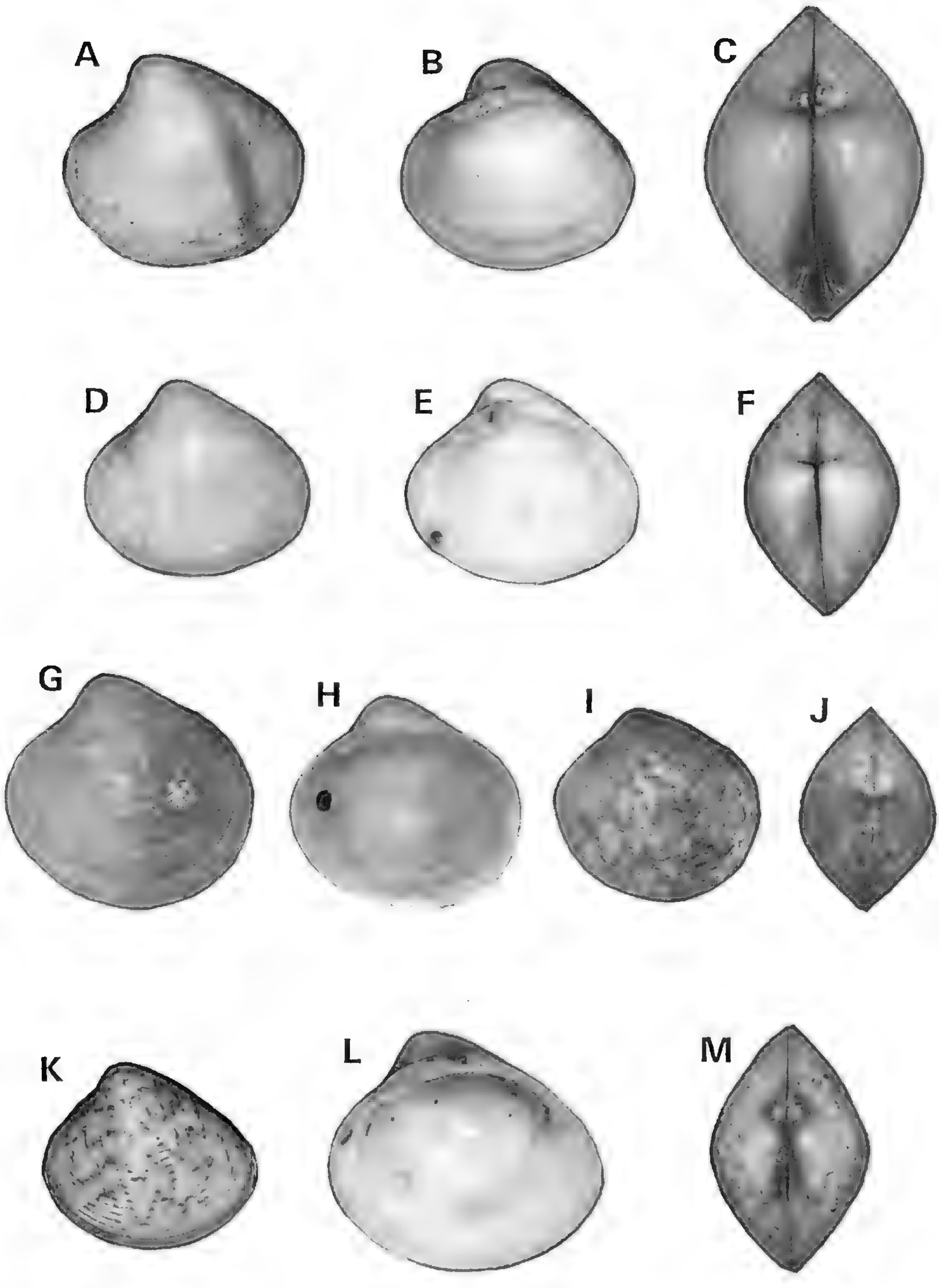

Fig. 11. *A–C, Lioconcha melharteae* Lamprell & Stanisic, 1996, New Caledonia, KL, 78 m, length 20.2 mm: *A*, external view lv; *B*, internal view rv; *C*, dorsal view pv. *D–F, Lioconcha caledonensis* Harte & Lamprell, 1999, Secteur de Belep, New Caledonia, KL, length 21 mm: *D*, external view lv; *E*, internal view rv; *F*, dorsal view pv. *G–J, Lioconcha richerdeforgei* Lamprell & Stanisic, 1996, Secteur de Pouebo, KL: *G*, length 9.9 mm, external view lv; *H*, length 9.18 mm, internal view rv; *I,J*, length 8 mm: *I*, external view lv; *J*, dorsal view pv. *K–M, Lioconcha gordoni* (E. A. Smith, 1885), Nada Bay, Viti Levu, Fiji, KL, length 14.6 mm: *K*, external view lv; *L*, internal view rv; *M*, dorsal view pv.

Distribution and habitat

Known only from New Caledonia, in sand to 127 m.

Remarks

The thin, strongly inflated, closely ridged valves, featuring a single orange ray posteriorly and an orange dorsal margin and lunule make this a very distinctive species. *Lioconcha melharteae*, as now redefined, is unlikely to be confused with any other species of *Lioconcha*. In their original description, Lamprell and Stanisic (1996) included, together with typical *L. melharteae*, less inflated specimens that lacked the orange colouration of ray, dorsal margin and lunule. Subsequently, Harte and Lamprell (1999) described these specimens as *L. caledonensis*. Although *L. caledonensis* shows a similar ridged sculpture to *L. melharteae*, it differs in having less inflated valves (narrowed posteriorly) and a pattern of widely scattered brown flecks on its white shell. The two species occur sympatrically off New Caledonia, but have yet to be collected outside this region. Sculptural and, especially, colour pattern and valve profile differences easily separate *L. melharteae* from other species within the heavily ridged *Lioconcha* group, such as *L. philippinarum*, *L. richerdeforgesi* and *L. trimaculata*.

Lioconcha caledonensis Harte & Lamprell, 1999

(Figs 11*D–F*, 14*E*, 16*D*)

Lioconcha (*Sulcilioconcha*) *caledonensis* Harte & Lamprell, 1999: 97, (type locality: New Caledonia, Secteur des Belep, stn 1103, 19°43′S, 163°57′E).

Material examined

Holotype. New Caledonia: Secteur des Belep: stn 1103, 19°43′S, 163°57′E (1pv) 32 m, MNHN.

Paratypes. New Caledonia: Secteur des Belep: same data as holotype (2pv, 2 rv, 1lv); stn 1129, 19°29′S, 163°49′E (7pv); stn 1117, 19°38′S, 163°54′E (5pv) 40 m; stn 1168 (1lv); Lagon Nord: stn 484, 19°00′S, 163°35′E (1pv) 35 m; stn 517, 19°09′S, 163°35′E (2pv) 42 m; stn 522, 19°08S, 163°38′E (4pv) 42 m, MNHN; stn 1129, 19°29′S, 163°49′E, 40 m, AMS C.312630 (1pv).

Diagnosis

Shell solid, ovate–trigonal, moderately inflated, solid, glossy; umbones strongly prosogyrate; lunule heart-shaped to lanceolate, raised, well delineated by incised line; shell with a weakly defined fold extending from umbones to the posteroventral margin. Sculpture of fine growth striae dominated by crowded, raised concentric ridges developed as rounded ribs, which become slightly wrinkled or disjunct at the anterior and posterior extremities; rib interstices narrow, shallow. Colour externally cream-white with sparse, obscure, irregularly spaced lines and small triangles; umbones and lunule white; shell internally white. Shell length to 18.5 mm.

Distribution and habitat

Known only from New Caledonia, in coarse sand to 42 m.

Remarks

This species is most similar to *Lioconcha. melharteae*, especially in relation to size (maximum 20 mm) and the structure of the close-set concentric ridges (see also Remarks for *L. melharteae*). However, *L. caledonensis* differs in having valves that are markedly

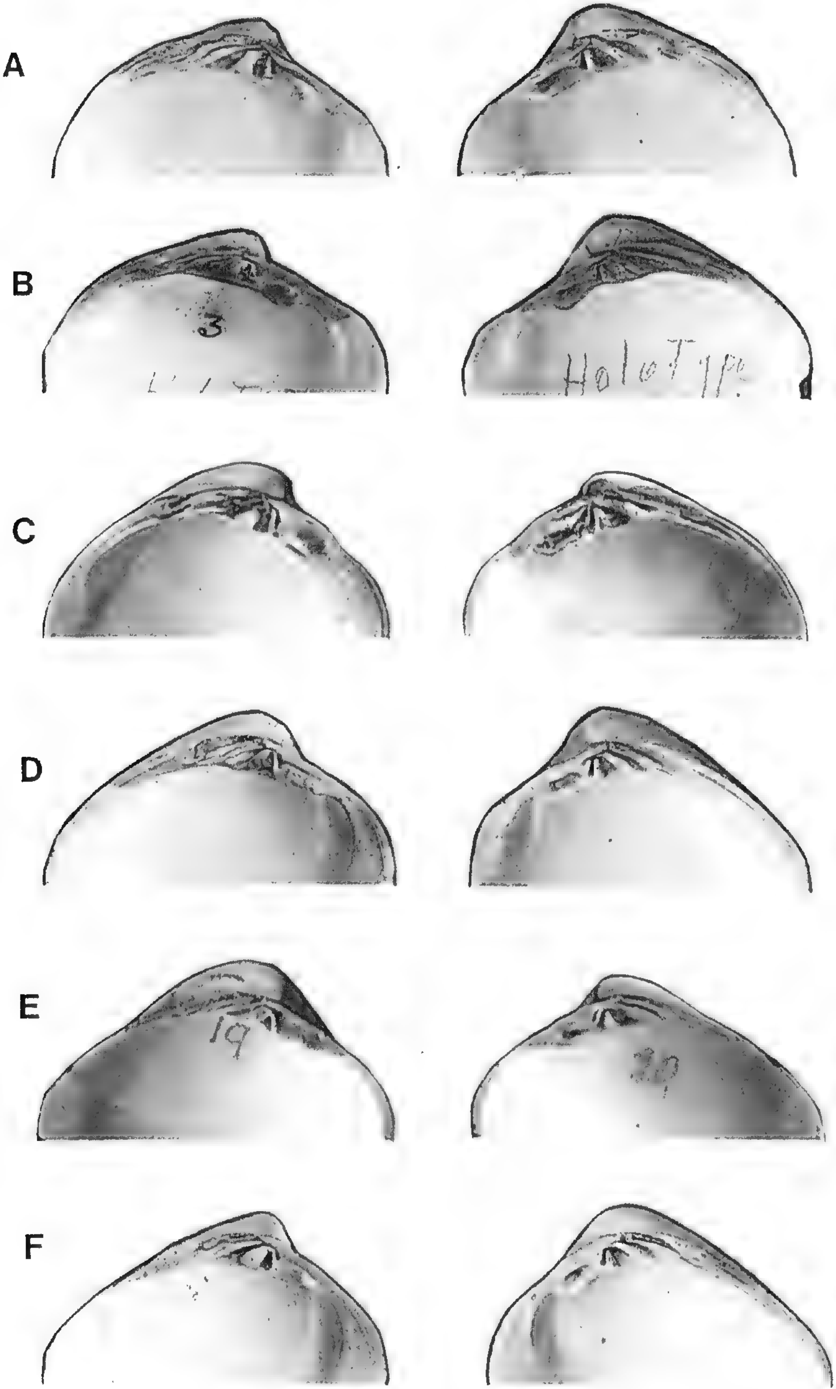

Fig. 12. Hinge plate and hinge teeth (lv and rv, on left and right, respectively). *A*, *Lioconcha castrensis* (Linnaeus, 1758) Little Trunk Reef, KL, length 49.5 mm. *B*, *L. macaulayi* n. sp., holotype Crouy Reef, New Caledonia, AMS C.204232, length 43.7 mm. *C*, *L. hieroglyphica* (Conrad, 1837), Kaneohe Bay, Oahu, AMS C.061304, length 41.5 mm. *D*, *L. tigrina* (Lamarck,1818), Mauritius, QM MO.11230, 37.9 mm. *E*, *L. fastigiata* (Sowerby,1851), Palm Is., KL, length 27.7 mm. *F*, *L. annettae* Lamprell & Whitehead, 1990, Lady Musgrave Island, in lagoon, KL, length 37 mm.

thicker, less inflated and more angulate in shape than those of *L. melharteae*. Moreover, the brown-flecked, poorly developed colour pattern of *L. caledonensis* contrasts with the predominantly white shell of *L. melharteae*, which is coloured by a single, large orange ray posteriorly and an orange dorsal margin and lunule. Other heavily ridged *Lioconcha* species (*L. philippinarum*, *L. richerdeforgesi*, *L. trimaculata* and *L. gordoni*) differ substantially in colour pattern, size and valve shape from *L. caledonensis* and are unlikely to generate any confusion.

Lioconcha richerdeforgesi Lamprell & Stanisic, 1996

(Figs 11*G–J*, 14*F*, 16*E*)

Lioconcha (*Sulcilioconcha*) *richerdeforgesi* Lamprell & Stanisic, 1996: 36, (type locality: New Caledonia, Secteur de Pouebo, Lagon, stn 876, 20°35′S, 164°51′E, 30–70 m).

Material examined

Holotype. New Caledonia: Secteur de Pouebo, Lagon (1pv) stn 876, 30–70 m, 20°35′S, 164°51′E, 30–70 m, 13 Jan 1987, MNHN.

Paratypes. New Caledonia: Secteur de Poindimie Lagon (9lv, 8rv many juveniles), stn 830, 105–110 m, 20°49′S, 165°19′E, 10 Jan 1987, MNHN; Secteur de Pouebo, Lagon: stn 876, 30–70 m, 20°35′S, 164°51′E, 13 Jan 1987, AMS C.305575 (2pv, 1 rv, 1lv).

Other material examined. **Australia: Queensland**: Lindeman Island, AMS C.358028 (2rv); off Cairns, 192 m, AMS C.358030 (1lv); Michaelmas Cay 20 m, AMS C.358024 (5 rv, 2lv); St Crispins Reef, AMS C.46277 (6 rv, 1lv). **New Caledonia**: Plateau Chesterfield-Bellona, Chalcal 1, stn D21 MNHN (1lv); Grand Recif Sud, Lagon, stn 324 MNHN (1rv); Secteur des Belep, Lagon, stn 1104 MNHN (1rv).

Diagnosis

Shell very thin, ovate, smooth but not glossy; lunule lanceolate, raised, well delineated by incised line; sculpture of crowded, flattened concentric ridges tending to anastomose at margins; rib interstices narrow, shallow. Colour externally tan with a network of white solid triangular markings; umbones pink, lunule white; shell internally white with external colour patterns visible through shell surface; dorsal margin with external pattern crossing both valves. Shell length to 11.25 mm.

Distribution and habitat

New Caledonia and Queensland, in sand to 110 m.

Remarks

This is the smallest known species of *Lioconcha* and its combination of greatly reduced size, heavy triangle patterning, ovate valves and poorly projecting umbones easily separates it from other heavily ridged members of the genus. *Lioconcha gordoni* is also small, but can be distinguished from *L. richerdeforgesi* by having much coarser ridges, a zigzag pattern and a glossy surface. Of the other small, ridged species of *Lioconcha*, *L. caledonensis* is larger, less patterned and exhibits a longer lunule than *L. richerdeforgesi*, whereas *L. melharteae* has thin, very inflated valves and a distinctive colour pattern featuring a single large ray of orange and an orange dorsal margin. *Lioconcha philippinarum* varies little in valve shape or colour from juvenile to adult and is unlikely to be confused with *L. richerdeforgesi*.

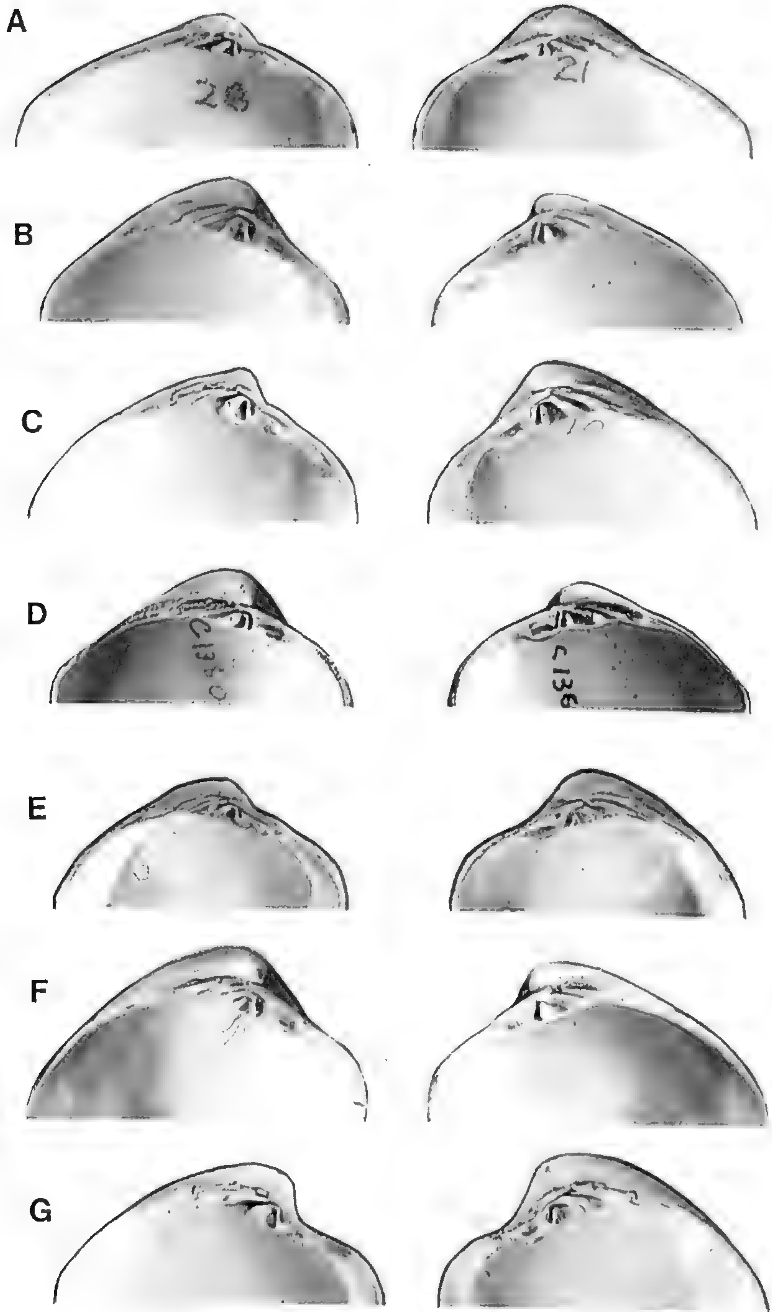

Fig. 13. Hinge plate and hinge teeth (lv and rv, on left and right, respectively). *A*, *Lioconcha pseudofastigiata* n. sp., holotype, Leyte, Philippines, AMS C.204480, length 34.5 mm. *B*, *L. ornata* (Dillwyn, 1817) Palm Passage, KL, length 33.7 mm. *C*, *L. ornata* (Dillwyn, 1817), Slasher's Reef, KL, 10 m, length 40.3 mm. *D*, *L. berthaulti* n. sp., holotype, Broadhurst Reef, E of Townsville, AMS C.136078, length 31.7 mm. *E*, *L. sowerbyi* (Deshayes, 1853*a*), Manilla Bay, Philippine Islands, QM MO.14505, length 32 mm. *F*, *L. polita* (Röding, 1798), MNHN, marked *Cytherea sulcatina* Lamarck var 2, specimen named by Lamarck, *C. sulcatina* Lamarck, 1817, holotype, MHNG 1084/24, length 42.2 mm. *G*, *Lioconcha schioettei* n. sp., Shelbourne Bay, KL, 52 m, length 32.7 mm.

Lioconcha gordoni (E. A. Smith, 1885), n. comb.

(Figs 11*K–M*, 14*G*, 16*E*)

Circe gordoni E. A. Smith, 1885: 146, (type locality: 22 m off Levuka, Fiji).

Material examined

Fiji: 16°57′S, 178°47′E, Nadi Bay, 9–35 m, AMS C.338106 (many); 5–19 fathoms, Nadi Bay, AMS C.67583 (in part) (3lv, 3rv). **Society Islands**: AMS C.379959 (1pv). **Sri Lanka**: 9–307 m, AMS C.379960 (1pv, 2lv).

Diagnosis

Shell trigonal, moderately inflated, moderately thin but strong, glossy; umbones strongly progyrate, projecting well above dorsal margins; extended and slightly rostrate posteriorly; moderately inflated; lunule heart shaped, well delineated by incised line. Sculpture of fine growth striae, usually dominated by numerous raised but rounded, concentric ridges developed as ribs (stronger marginally, of sometimes variable coarseness). Colour externally white with transverse zigzag red-brown lines; umbones white; lunule white with purple or mauve tinge peripherally; shell internally white, stained with large median blotch of mauve. Shell to length to 16.3 mm.

Distribution and habitat

Indo-West Pacific (but sporadic), in sand to 110 m.

Remarks

Examination of an extensive series of *Lioconcha gordoni* reveals that the strength and extent of the ribbing may vary and that specimens with poorly developed sculpture can occur in strongly ribbed populations. *Lioconcha melharteae* and *L. caledonensis* are both pale coloured, like *L. gordoni*, but both grow larger than *L. gordoni* and have a proportionately larger lunule. These species also differ from *L. gordoni* in their colour pattern: in *L. melharteae*, a posterior orange ray and orange dorsal margin; in *L. caledonensis*, two to three loosely defined speckled rays. *Lioconcha richerdeforgesi* is much thinner and usually considerably smaller than *L. gordoni* and, although also showing zigzag colour pattern, has ovate valves and low umbones. *Lioconcha dautzenbergi* is similar in size and zigzag colour pattern to *L. gordoni*, but has very thick ribs, less prosogyrate umbones and also exhibits tan rays externally. The compact, mauve-purple lunule of *L. gordoni* is also shared with *L. philippinarum* (a larger species showing a brown colouration with six to eight rays of darker brown), *L. dautzenbergi* and *L. trimaculata* and presumably indicates a close relationship between these species. Although originally placed in *Circe* Schumacher, 1817, by Smith (1885), *L. gordoni* is clearly referable to *Lioconcha*, and is herein transferred to that genus.

Discussion

The genus *Lioconcha* Mörch, 1853 has been divided into two subgenera: *Lioconcha sensu stricto* and *Sulcilioconcha* Habe, 1951. In erecting *Sulcilioconcha*, Habe (1951) gave the following diagnosis for the subgenus: '... shell purplish, thick, with remarkable, commarginal ribs' (English translation of the original Japanese text). He included only the type species *L. philippinarum* within *Sulcilioconcha*. Keen (1969) recognised both subgenera in the 'Treatise on Invertebrate Paleontology', but only cited the presence of

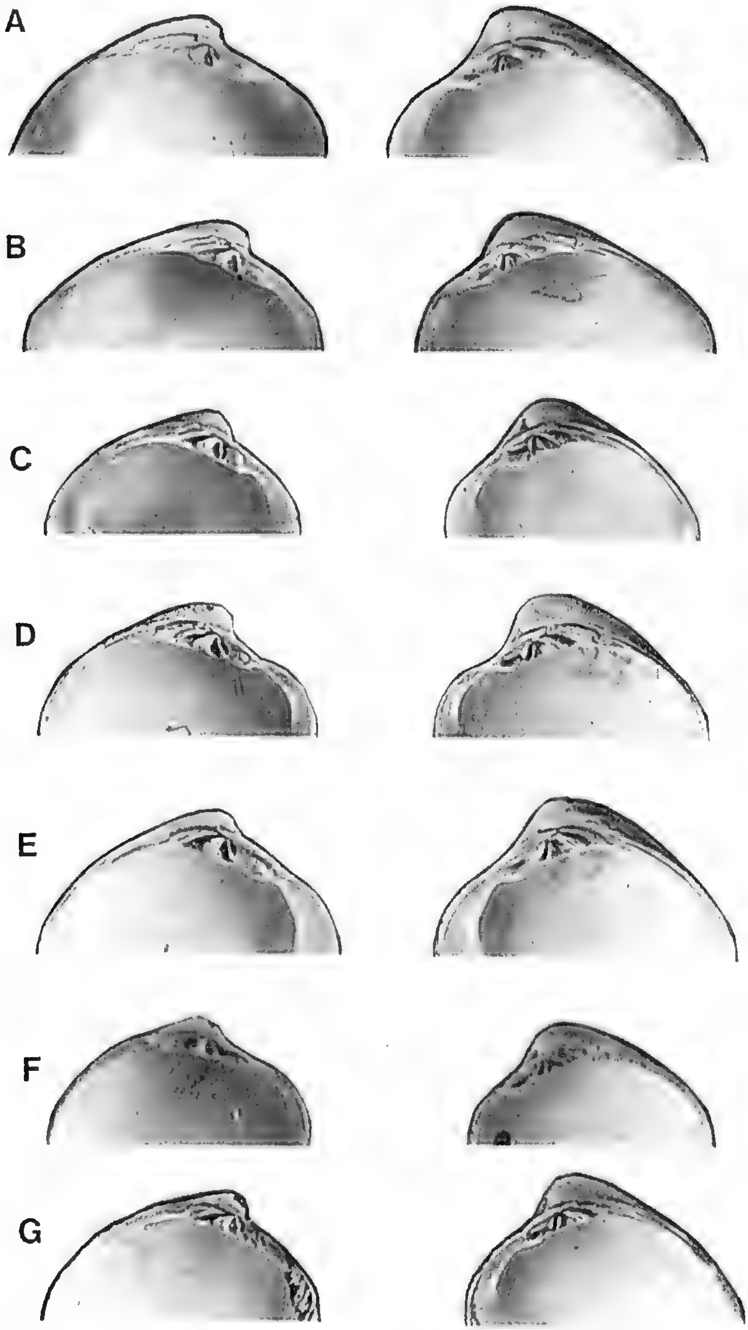

Fig. 14. Hinge plate and hinge teeth (lv and rv, on left and right, respectively). *A*, *Lioconcha trimaculata* (Lamarck, 1817), Philippines, KL, length 27.6 mm. *B*, *L. philippinarum* (Hanley, 1844), New Guinea, KL, length 29.2 mm. *C*, *L. dautzenbergi* (Prashad, 1932), holotype, ZMA.3.32.112, length 15.9 mm. *D*, *L. melharteae* Lamprell & Stanisic, 1996, New Caledonia, KL, 78 m, length 20.2 mm. *E*, *L. caledonensis* Harte & Lamprell, 1999, Secteur de Belep, New Caledonia, KL, length 21 mm. *F*, *L. richerdeforgesi* Lamprell & Stanisic, 1996, Secteur de Pouebo, KL, length 9.9 mm. *G*, *L. gordoni* (E. A. Smith, 1885), Nada Bay, Viti Levu, Fiji, KL, length 14.6 mm.

concentric ridges (and not shell colouration) in her diagnosis of *Sulcilioconcha*. As we have demonstrated in the present study, the external and often the internal colour of *Lioconcha* shells may vary considerably within and between species. Undoubtedly, valve colouration (both external and internal) is very useful in determining species identity within *Lioconcha*, but not as a key defining character for a subgenus (Habe's reference to a purplish shell for *L. philippinarum* is vague). Several species of *Lioconcha s.s.* may show varying degrees of development of concentric commarginal ridges, to the point that certain highly sculptured specimens of *L. annettae*, *L. schioettei* and *L. sowerbyi* would qualify for inclusion within *Sulcilioconcha* rather than *Lioconcha s.s.* Comparison of *L. schioettei* with *L. trimaculata* provides an excellent example highlighting the rather superficial nature of the subgeneric division. These two species show many conchological similarities (suggesting a close relationship) but, based on the stronger and more consistent development of concentric ridges in *L. trimaculata*, the two would have to be placed into different subgenera. In the case of the normally heavily ridged species *L. gordoni*, we have observed a marked degree of variation in the strength of the ridges, once again suggesting that any subgeneric division of *Lioconcha* based solely on external sculpture has no validity.

Although the precise relationship of *Lioconcha* to other pitarine genera remains to be clarified, in terms of general shell shape, teeth and hinge plate morphology, colour pattern and sculptural range, the group appears closest to *Pitar* Römer, 1857 and *Callista* Poli, 1791. However, *Lioconcha* differs markedly from these two genera in the extent of the pallial sinus, this feature being almost absent in *Lioconcha* and deep and clearly marked in *Pitar* and *Callista*.

The present study has shown that whereas most *Lioconcha* species, such as *L. philippinarum*, *L. melharteae* and *L. berthaulti* n. sp., show low or at least moderately low levels of external colour and pattern variation, others, such as *L. castrensis* and *L. ornata*, show very wide variation. In the latter examples, there is a real possibility that some variants may be worthy of taxonomic recognition and, alternatively, some nominal taxa (e.g. *L. annettae*) may prove to be colour variants of other species. The presence of occasional specimens seemingly intermediate between two sympatric species suggests the possible occurrence of local hybridisation (e.g. between *L. ornata* and *L. annettae* in waters off New Caledonia). Unfortunately, at present, comparative anatomical, reproductive and molecular data are lacking to probe the significance of colour and/or pattern variations within species of *Lioconcha*. Internal colouration can also vary within populations, sometimes more than external colour and/or pattern, but often such variation is associated with increasing age. Juvenile *L. schioettei* n. sp., for example, are often white to light yellow internally and only acquire the mauve posterior colouring with advanced adulthood (and, even then, the valves may occasionally retain their juvenile colour).

In terms of structural variation, we have observed that the umbones often become increasingly prosogyrate with age in a number of species (e.g. *L. ornata*, *L. annettae*, *L. fastigiata* and *L. castrensis*). Usually this occurs as the result of the posterior extremity becoming more attenuated. However, in adults of *L. castrensis* of the 'hieroglyphic' pattern, large individuals have more circular valves (height and length almost equal) compared with the anteriorly–posteriorly elongate juveniles from the same population (valves longer than high). In addition, we have seen evidence of stunting of the posterior extremity, presumably through interaction of the living animal with a less than optimal sediment type. Such valve shape changes reduce the value of length : height ratios for taxonomic discrimination if the primary goal is to uneqivocally define a species throughout all its growth stages (unless one is comparing similar sized specimens of different species).

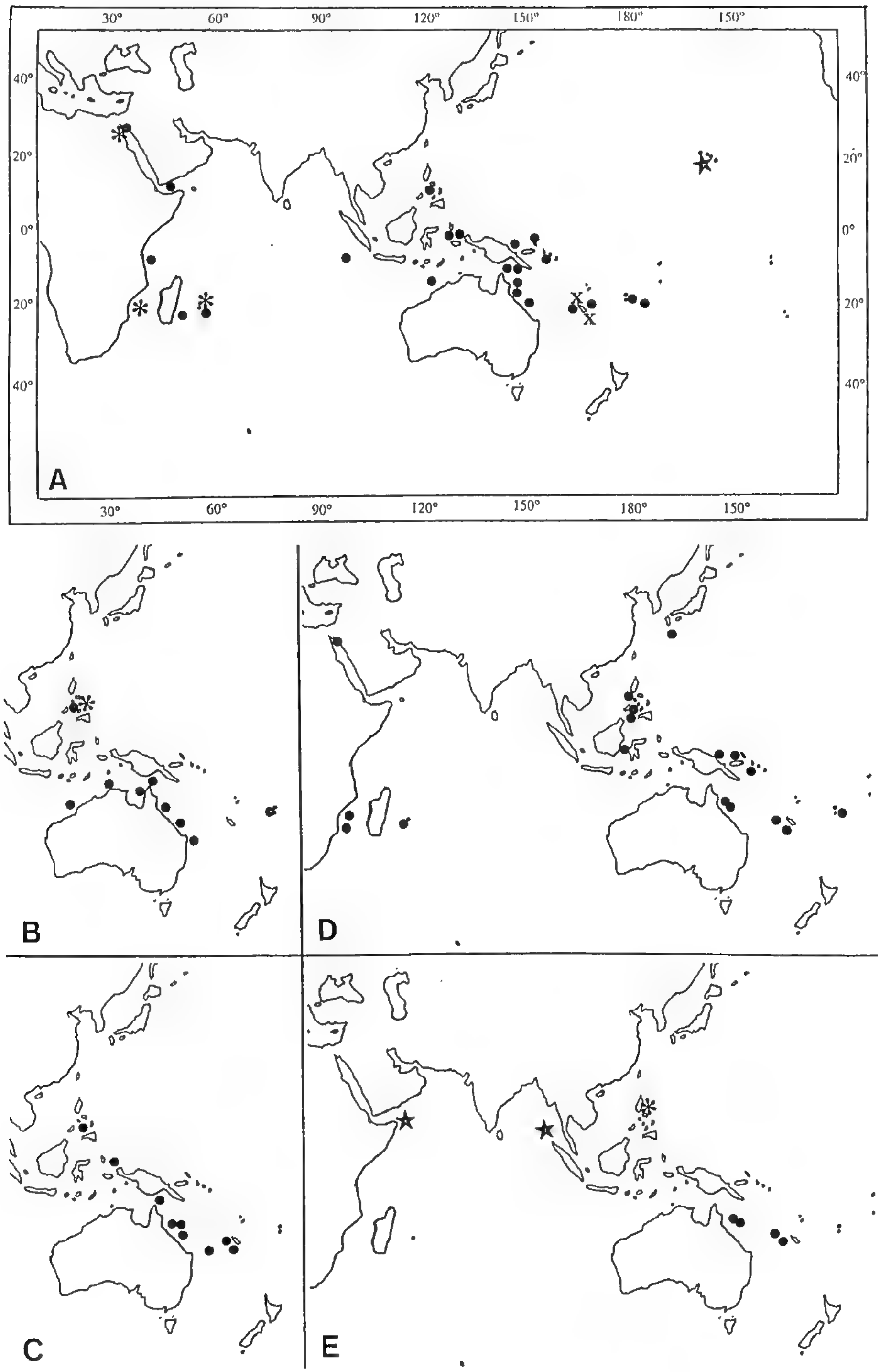

Fig. 15. Distribution. *A*, *Lioconcha castrensis* (Linnaeus, 1758) (●); *L. macaulayi* n. sp. (X), *L. hieroglyphica* (Conrad, 1837) (★), *L. tigrina* (Lamarck, 1818) (∗). *B*, *L. fastigiata* (Sowerby, 1851) (●), *L. pseudofastigiata* n. sp. (∗). *C*, *L. annettae* Lamprell & Whitehead, 1990 (●). *D*, *L. ornata* (Dillwyn, 1817) (●). *E*, *L. sowerbyi* (Deshayes, 1853) (∗), *L. polita* (Röding, 1798) (★), *L. berthaulti* n. sp. (●).

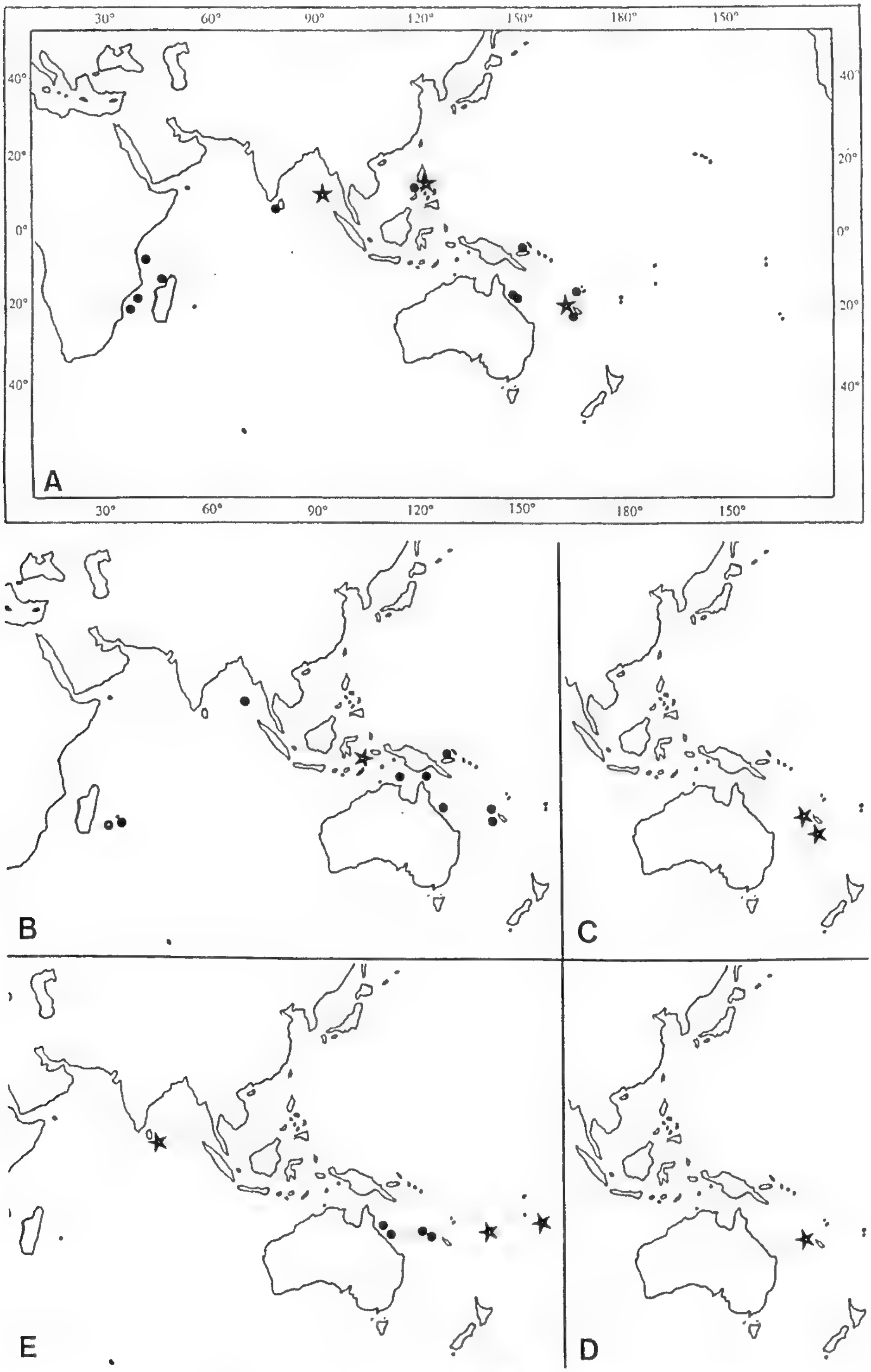

Fig. 16. Distribution. *A*, *Lioconcha schioettei* n. sp. (●), *L. trimaculata* (Lamarck, 1817) (★). *B*, *L. philippinarum* (Hanley, 1844) (●), *L. dautzenbergi* (Prashad, 1932) (★). *C*, *Lioconcha melharteae* Lamprell & Stanisic, 1996 (★). *D*, *L. caledonensis* Harte & Lamprell, 1999 (★). *E*, *L. richerdeforgei* Lamprell & Stanisic, 1996 (●), *L. gordoni* (E. A. Smith, 1885) (★).

The restricted distribution of several species, such as *Lioconcha macaulayi* n. sp., *L. melharteae*, *L. richerdeforgesi* and *L. berthaulti* n. sp., invites discussion. We are unaware of any studies of the length of time spent by larval *Lioconcha* in the water column prior to settlement. However, it would be of considerable interest to determine whether the seemingly high degree of endemicity exhibited by several *Lioconcha* species is due to a very abbreviated pre-settlement time (i.e. drifting time spent by veligers in the water column and under the dispersal influence of water currents) or is simply the product of patchy collection effort (many areas of the Western Pacific remain unsampled or poorly sampled). Conceivably, both factors are involved but, if sediment type plays any significant role in settlement success (and the effects of valve stunting, and variation in sculpture strength both hint that this is may be so), then there would a clear selective advantage in having a short larval pre-settlement time. Short pre-settlement times, combined perhaps with localised current eddies, would enhance the prospects of speciation by limiting genetic exchange between populations, as opposed to long pre-settlement times, which would enhance genetic exchange and expand species ranges (see, for example, Scheltema 1971, 1986). High levels of endemicity appear to be characteristic of the Australian Veneridae in general, with endemics making up 43% of all venerid species recorded in the fauna (Harte 1998). We anticipate that future studies, especially molecular genetics and field observations on live animals, in combination with comparative work on reproductive habits (including comparative larval settlement studies), will aid greatly in resolving taxonomic difficulties within the genus *Lioconcha*. Controlled breeding experiments between conspecifics and between nominal taxa would also prove a worthwhile exercise, if only to determine the level of colour and pattern variation possible from a single mating pair. Attention for future work should be focused particularly on the variable *L. castrensis* and the exceedingly variable *L. ornata*, with special attention being paid to distinct colour and shape variants.

Key to extant species of *Lioconcha*

Although most species of *Lioconcha* are relatively constant in colour pattern, some of the larger-sized (30–55 mm) species may exhibit significant variation, even at a single collection site. Certain structural features also alter with age, such as the position of umbones in relation to the anterior and posterior extremities and the size of hinge teeth. External colour pattern and internal colour also often vary to some extent between size classes in some species. The following key is intended to be used in conjunction with the plates and text. It should be expected that occasional specimens may prove difficult or impossible to determine accurately, especially in the case of extremely juvenile or worn and bleached material. The key is largely intended for the identification of late juvenile to mature specimens (the size ranges given for each species are indicative of adult specimens). In general, we have emphasised the most accessible and constant shell features, but have also attempted to accommodate any variation in features based on the material available for study.

1. External colouration of shell with a single, broad orange ray posteriorly 2
   External colouration of shell lacking a single, broad orange ray 3
2. Shell smooth; tented-reticulate background colour; lunule white or pink; dorsal margin speckled .... *L. berthaulti* (20–30 mm) (Figs 7*J–N*, 13*D*, 15*E*)
   Shell with raised, concentric ridges; white background colour; orange lunule and dorsal margin .... *L. melharteae* (10–15 mm) (Figs 11*A–C*, 14*D*, 16*C*)
3. Raised ridges present over all or most of valve surface 4
   Raised ridges absent or evident only on marginal regions of valves 9
4. Lunule or perilunular area (and usually dorsal margin) purple-brown in colour 5
   Lunule and perilunular area white, patterned or brown/black; dorsal margin white or patterned 7

5. Shell smooth but not glossy; fine raised ridges externally; internally usually with brown blotch associated with each adductor scar .... *L. trimaculata* (20 mm) (Figs 10*A–F*, 14*A*, 16*A*)
   Shell glossy; coarse raised ridges externally; internally, colour patches not associated with one or either adductor scars 6
6. Shell externally chestnut brown, with two to five darker brown rays and sometimes faint zigzags; dorsal margin brown or purple-brown; internally white with light brown blotch under umbones .... *L. philippinarum* (20–30 mm) (Figs 10*G–L*, 14*B*, 16*B*)
   Shell externally white overlain with zigzag reticulations; dorsal margin white or with some line patterning; internally white with brown/purple blotch mid-valve .... *L. gordoni* (10–15 mm) (Figs 11*K–M*, 14*G*, 16*E*)
   Shell externally white overlain with broad bands or brown and zigzag reticulations; dorsal margin purple-brown; internally white with purple patch mid-valve and brown on posterior adductor scar .... *L. dautzenbergi* (10–15 mm) (Figs 10*M,N*, 14*C*, 16*B*)
7. Shell minute; rounded; thin and fragile; fine, concentric raised ridges developed as fine ribs; white tented reticulate pattern on tan externally...... *L. richerdeforgesi* (5–8 mm) (Figs 11*G-J*, 14*F*, 16*E*)
   Shell small, robust, well developed, concentric raised ridges developed as ribs; externally white with small, scattered, faint tent markings............. *L. caledonensis* (10–20 mm) (Figs 11*D-F*, 14*E*, 16*D*)
   Shell moderately to very large (20–55 mm), robust to moderately thin; concentric raised ridges clearly marked or subdued; externally tan to brown, pattern of fine, diffuse zigzags 8
8. Posterior–ventral margin showing sinuation; umbones slightly to moderately prosogyrate; lunule weakly delineated by incised line; internally white to yellow, usually with mauve-purple staining posteriorly .... *L. schioettei* (30–40 mm) (Figs 9*K–P*, 13*G*, 16*A*)
   Posterior–ventral margin evenly convex; umbones slightly to moderately prosogyrate; lunule weakly delineated by incised line; internally white with extensive postero-ventral brown staining .... *L. sowerbyi* (25–35 mm) (Figs 8*A–N*, 13*E*, 15*E*)
   Posterior–ventral margin evenly convex; umbones strongly prosogyrate; lunule well delineated by incised line; internally white, often with some median brown staining .... *L. polita* (30–40 mm) (Figs 9*A–J*, 13*F*, 15*E*)
9. Lunule raised, well delineated by deeply incised line 10
   Lunule flat, poorly delineated by incised line 12
10. Shell with abruptly truncate posterior margin; heart-shaped lunule; valves externally white overlain with sparse, irregular tents or blotches, most of which appear smudged and diffuse .... *L. macaulayi* (40–50 mm) (Figs 2*A–O*, 12*B*, 15*A*)
   Shell with rounded posterior margin; heart-shaped to lanceolate lunule; valves externally white to grey-white with well-defined markings 11
11. Shell circular to ovate; umbones slightly progyrate; externally valves with variable pattern of tents, zigzags or rods (or a mixture of these) .... *L. castrensis* (30–55 mm) (Figs 1*A–K*, 12*A*, 15*A*)
   Shell ovate–trigonal; umbones markedly prosogyrate; externally valves with rod or angular markings .... *L. hieroglyphica* (40–50 mm) (Figs 3*A–L*, 12*C*, 15*A*)
12. Ridges clearly marked on ventral third of valve 13
   Shell lacking or essentially lacking ridge sculpture (i.e. growth striae only) 14
13. Colour pattern composed of many, open brown tents of varying sises (pointing away from the umbones), often diffuse (and with patches of grey); umbones not markedly raised above hinge line .... *L. annettae* (30–40 mm) (Figs 5*K–P*, 12*F*, 15*C*)
   Colour pattern composed of solid tents (pointing towards the umbones) of reddish-brown on a white background, the tents often amalgamating ventrally into coarse, angled rays; umbones markedly raised above hinge line .... *L. tigrina* (30–40 mm) (Figs 4*A–N*, 12*D*, 15*A*)
14. Colour pattern externally of heavy, open black-brown tents often interconnected; rays of colour never present externally; lunule with black-brown blotch umbonally; shell internally white often flesh coloured umbonally .... *L. fastigiata* (20–40 mm) (Figs 5*A–J*, 12*E*, 15*B*)
   Colour pattern externally of solid black-brown tents sometimes connected; rays of colour never present externally; lunule with black-brown blotch umbonally; shell internally white, often flesh coloured umbonally, always with broad, diffuse purple-brown ray or blotch medially .... *L. pseudofastigiata* (25–34 mm) (Figs 6*A–G*, 13*A*, 15*B*)
   Colour pattern externally of small to minute open tents of brown, very commonly intersected by rays of brown or white; lunule lacking black-brown blotch umbonally; shell internally white to orange .... *L. ornata* (25–45 mm) (Figs 7*A–I*, 13*B,C*, 15*D*)

Acknowledgments

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Observations on the behaviour of the Australian land snail *Hedleyella falconeri* (Gray, 1834) (Pulmonata: Caryodidae) using the spool-and-line tracking technique

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Abstract

A brief field study of the Australian caryodid land snail *Hedleyella falconeri* (Gray, 1834), using the spool-and-line tracking method, provided detailed information concerning patterns of nocturnal movement and types of diurnal shelter site, as well as egg laying and foraging activities. *Hedleyella falconeri* was active on 74% of nights observed and, when active, moved an average of 8.70 m per night (maximum of 21.72 m in a single night), with an average straight-line displacement of 5.10 m per night (maximum of 13.96 m in a single night). Snails were more likely to be active and to move further in wet weather than dry weather. They appeared to be nomadic, moving randomly around the forest floor, with no homing behaviour observed and, contrary to preconceptions, no apparent active selection of secure diurnal shelter sites, such as beneath fallen timber. A description of diurnal shelter sites is provided, together with a description of the eggs and egg laying behaviour and observations on diet. The behaviour of *H. falconeri* is considered to reflect its equable rainforest habitat, with implications for its continued conservation. The present study demonstrates the considerable value of the spool-and-line tracking method in the field study of larger land snail species.

Additional keywords: diurnal shelter, egg laying, movement, rainforest.

Introduction

Numerous summaries of the status of research concerning the Australian land snail fauna over the past four decades have noted a paucity of ecological and biological studies. McMichael and Iredale (1959) noted that whereas the taxonomic study of Australia's land and freshwater Mollusca was far from complete, their ecology had received practically no attention. Bishop (1981) noted that the majority of Australian land snail research had focused on taxonomic studies based largely on shell morphology, to the neglect of biological or ecological studies of the living animals. Smith (1992) noted that a large proportion of Australia's terrestrial and freshwater mollusc species had never been observed in their natural habitat, with no information available on even their basic biology. Ponder (2000) noted that basic biological information for Australian molluscs was lacking for all but a few taxa. Many species of land snail in Australia and throughout the world are considered to be declining and at risk of extinction (Wells 1988; Ponder 1997; IUCN 2000). An understanding of their basic biological and ecological requirements is essential if land snails are to be properly considered in conservation and land use planning decisions.

The present project was undertaken as a pilot study to examine the feasibility and value of the spool-and-line tracking technique in studying movement patterns and shelter site selection by the Australian caryodid land snail *Hedleyella falconeri* (Gray, 1834). This technique involves attaching a small spool of thread to the subject animal, which unwinds from the inside as the animal moves about, leaving a trail of thread that can be subsequently followed to trace movement and relocate the animal. The technique is technologically

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Fig. 1. *Hedleyella falconeri* is Australia's largest native land snail and is common in rainforests in north-east NSW and south-east Queensland.

simple and low cost, but very data rich, providing a continuous and detailed record of movement over the tracking period. The spool-and-line technique has been used to study spatial and temporal patterns of habitat usage in vertebrates ranging from frogs and small reptiles to medium sized mammals (Miles *et al.* 1981; Boonstra and Craine 1986; Stott 1987; Anderson *et al.* 1988; Manning and Ehmann 1991; Carthew 1994; Key and Woods 1996). Pearce (1990) previously demonstrated and discussed the value of spool tracking in the study of land snails, noting how the technique could provide information concerning activity range, dispersal capacity, homing behaviour, behavioural interactions (such as mucous trail following) and the location of refuge and nesting sites. To the author's knowledge, the present study represents only the second use of the spool-and-line technique in studying land snails and the first for an Australian land snail species.

Hedleyella falconeri (Fig. 1) is a large land snail found in ground litter in rainforest and tall open forest from Mount Mee, south-east Queensland, to the Hunter Region in northern New South Wales (Cox 1868; Iredale 1943; Smith 1992). It is Australia's largest native land snail, with a helicoid shell up to 9–10 cm in size (Shea 1978; Abbott 1989). Despite being a large, well known species with a distribution in the highly populated eastern coastal region, little published information is available concerning its ecology and behaviour. Shea (1978) noted that *H. falconeri* was nocturnal, hiding by day under logs, heaps of leaves and sticks. Bishop (1981) described *H. falconeri* as a ground feeding species, not climbing more than 50 cm or so. He noted that it was very difficult to find by day, with a preference for giant strangler figs as diurnal shelter sites, but easily found at night on the ground around fig trees. Additional anecdotal information on the behaviour and ecology of *H. falconeri* is recorded in the unpublished newsletter of the Malacological Society of Australasia (Jahnsen 1967). This includes observations on activity patterns and movement, comments on diurnal shelter site selection and frequency of predation by ground foraging rainforest birds, as well as a

description of the nest site and eggs. Previous opportunistic observations by the present author suggested that *H. falconeri* was most likely to be active on wet nights, that activity was limited to ground level, that, by day, animals were most commonly found sheltering under fallen timber and that the species was a common prey item of the noisy pitta, *Pitta versicolor* (Pittidae), a diurnal ground litter foraging rainforest bird species.

The above observations and comments provide some insight into the ecology of *H. falconeri*; however, being typically based on anecdotal or opportunistic sightings, they are subject to potential observer bias and subjectivity. The present spool-and-line tracking study enabled the collation of a dataset of continual observations of movement patterns and diurnal shelter site selection over a period of approximately 2 weeks. These quantitative and qualitative findings have been compared with previous anecdotal or opportunistic information.

Materials and methods

The study area was located in Bruxner Park Flora Reserve (30°15′S 153°06′E), near Coffs Harbour on the north coast of New South Wales, Australia. The study area was approximately 60 × 30 m in area and was located adjacent to Bucca Bucca Creek in the central part of the Reserve, at an elevation of 140 m Australian height datum. The vegetation of the study site was subtropical rainforest with scattered emergent flooded gum, *Eucalyptus grandis*. One mature strangler fig, *Ficus watkinsiana*, was present within the study area. The ground surface was covered by a layer of leaf litter and scattered rotting logs.

Nocturnal searches for *H. falconeri* in the study area were undertaken over two consecutive nights during a period of wet weather in mid-February 2000. Each search was of approximately 1 h duration and involved looking for active snails with the aid of a 50 watt spotlight. Two adult snails were found active on the forest floor in the study area on the first night and a third was found on the second night. The three snails were measured, weighed and marked with an identifying number on the shell (Table 1). (Note, the three snails were numbered 2, 3 and 4 because one snail in the study area had previously been marked as snail 1 in an earlier unsuccessful tracking attempt using a rotating spool system.) A spool of fine nylon thread (Danfield bobbin no. 10 white; Penguin Threads, Prahran, Victoria, Australia) wrapped in electrical tape was affixed to the rear of each animal's shell using electrical tape and cyanoacrylate 'super glue' (Fig. 2). Spools weighed 5 g and measured 38 mm long and were 16 mm in diameter at the middle, tapering to 11–12 mm diameter at each end. The snails were released at point of capture within 15 min of collection, with the free end of the thread secured to a stick in the ground next to the snail.

The study site was visited daily each morning for 17 days following marking of the snails (16 days for the snail marked on the second night), giving a total dataset of 50 nights of spool tracking data from the three tracked snails. On each visit the thread trail of each animal was traced and interpreted for activity and the animal located. The actual distance travelled (length of spool thread trail) and straight-line displacement over the previous night was measured, the location of the animal was marked and mapped, and notes were made on overnight activity and diurnal shelter site.

An additional two *H. falconeri* specimens found in the study area during the spool tracking study were also individually marked (as snails 5 and 6) and observations on their behaviour noted.

Information on the weather conditions over the course of the spool tracking study was recorded. There were 8 nights during the study when weather conditions in the study area were wet and 9 nights with dry conditions. This equated to 23 wet snail nights and 27 dry snail nights for the pooled dataset of 50 snail nights.

At the end of the 17 day study period, the spools were removed and the snails were released at last point of collection. The straight-line distance between each snail's last point of collection and original point of collection was measured to provide the straight-line displacement over the entire spool tracking study. Identification numbers were left on the animals so that they could be identified on subsequent inspections.

Nocturnal searches in the study area and adjacent areas were undertaken during or following rain on three subsequent occasions in an attempt to relocate the five marked snails and determine the straight-line displacements over longer periods. One search was in late March 2000 (24 nights since removal of spools), one in late May 2000 (87 nights since removal of spools) and one night in late December 2000 (303 nights since removal of spools). The search effort each night was between 30 and 60 min. When a snail was found, its location was marked for future reference and the straight-line distance between its current and last recorded location was measured. Two marked snails were relocated in late March, of which one was found again in late May. No marked snails were found in late December.

Table 1. Size of snails observed in the present study
Note: shell height and width are straight-line measurements using calipers

Animal	Weight (g)	Shell height (mm)	Shell width (mm)
Snail 2	118.5	75.2	54.0
Snail 3	118.0	81.6	53.3
Snail 4	68.5	62.9	43.4
Snail 5	–	–	–
Snail 6	–	72.2	49.3

Fig. 2. *Hedleyella falconeri* with spool attached to enable tracking. The 50 cent coin shows the scale.

Results

Movement of snails

A combined total of over 320 m of movement by the three spool tracked snails was recorded over the 50 snail nights comprising this study. The tracking spatial data for the three snails (snails 2, 3 and 4) is shown in Fig. 3. The location of each of the two additional snails (snails 5 and 6) found in the study area during the spool tracking study is also shown. The area of movement mapped for snail 2 did not overlap with any other identified snail. Snails 3 and 4 had partially overlapping areas of movement but did not meet. Snail 3 was found sheltering with one of the additional snails (snail 6) on 1 day, but had moved on by the following day, while snail 6 remained there for another 2 days, as described under breeding observations below.

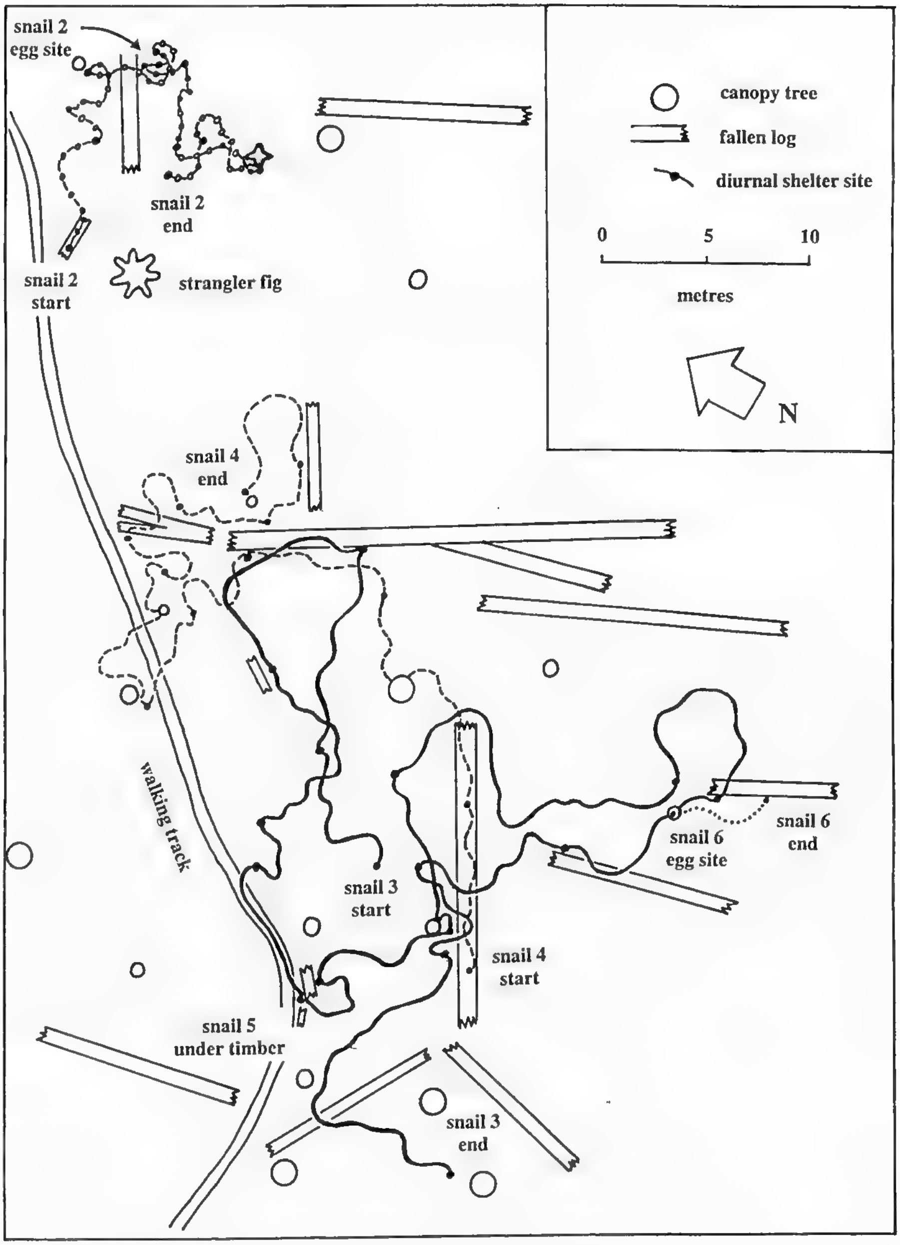

Fig. 3. Map of the study area showing movement patterns and diurnal shelter sites of three spool-tracked *Hedleyella falconeri*. The location of two additional *H. falconeri* found in the study area is also shown, together with the approximate location of the two nest sites recorded in the present study.

Average distances moved per night by each snail in wet and dry conditions during the spool tracking are shown in Table 2. Data were randomly deleted to give a balanced dataset of 7 nights per snail (three snails) per weather type (wet or dry) for statistical analysis. A two factor analysis of variance of this data indicated that there was a significant difference between the snails ($F = 14.19$ with 2, 36 d.f., $P<0.01$) and a significant difference between wet and dry nights ($F = 10.71$ with 1, 36 d.f., $P<0.01$), with no significant interaction

Table 2. Average distances travelled per night by snails during spool tracking study (mean ± SEM)

	Snail 2	Snail 3	Snail 4
Wet nights	3.64 ± 0.97 m (8 nights)	13.89 ± 1.45 m (8 nights)	8.62 ± 2.28 m (7 nights)
Dry nights	1.72 ± 0.80 m (9 nights)	7.90 ± 1.78 m (9 nights)	3.86 ± 1.24 m (9 nights)

Table 3. Average straight-line displacements per night by snails during spool tracking study (mean ± SEM)

	Snail 2	Snail 3	Snail 4
Wet nights	2.41 ± 0.67 m (8 nights)	8.39 ± 1.06 m (8 nights)	5.14 ± 1.46 m (7 nights)
Dry nights	0.99 ± 0.54 m (9 nights)	3.75 ± 0.96 m (9 nights)	2.55 ± 0.88 m (9 nights)

between these factors (F = 1.34 with 2, 36 d.f., P>0.05). It was therefore concluded that individual snails differed in the average distances moved overnight, but that all snails tended to move further on wet nights than dry nights. The greatest overnight movement recorded during the study was 21.72 m by snail 3 on a wet night.

Average straight-line displacements per night by each snail in wet and dry conditions during the spool tracking study are shown in Table 3. Data were randomly deleted, as above, to give a balanced dataset for statistical analysis. A two factor analysis of variance of this data indicated that there was a significant difference between the snails (F = 8.41 with 2, 36 d.f., P<0.01) and a significant difference between wet and dry nights (F = 15.17 with 1, 36 d.f., P<0.01), with no significant interaction between these factors (F = 3.07 with 2, 36 d.f., P>0.05). It was therefore concluded that individual snails differed in the average straight-line displacements overnight, but that all snails tended to move further on wet nights than dry nights. The greatest overnight straight-line displacement recorded during the study was 13.96 m by snail 3 on a wet night.

Zero overnight movement by a spool tracked snail was recorded on 13 occasions. Three of these (23.1%) were on wet nights, whereas 10 (76.9%) were on dry nights. A Chi-square 'goodness of fit' analysis indicated that these observed proportions were significantly different from that expected on the basis of the relative number of wet snail nights (46%) and dry snail nights (54%) experienced during the study (χ^2 = 21.1 with 1 d.f., P<0.01). It was therefore concluded that snails were more likely to remain inactive on dry nights than wet nights.

Overall, tracked snails were active on 74% of snail nights observed and, when active, moved an average of 8.70 m per night, with an average straight-line displacement of 5.10 m per night. Snails were significantly more likely to be active and to move greater distances on wet nights than dry nights.

A summary of distances moved and straight-line displacements by the three snails tracked during the spool-and-line study is provided in Table 4. The index of daily directness of movement (indicating the degree to which once-daily straight-line measurements reflected actual movements) was similar for the three snails, ranging only from 55.3% (snail 3) to 63.1% (snail 2). In contrast, the index of directness of movement over the entire study

Table 4. Summary comparison of distances moved and straight-line displacements during and following the spool-and-line study

	Snail 2	Snail 3	Snail 4
Duration of spool tracking (nights)	17	17	16
Sum daily distances moved during spool tracking (m)	44.64	182.24	95.07
Sum daily straight-line displacements during spool tracking (m)	28.16	100.84	58.92
Index of daily directness of movement (sum daily straight-line displacements/sum daily movements; %)	63.1	55.3	62.0
Overall straight-line displacement from start to end of spool tracking (m)	6.10	16.22	25.50
Index of directness of movement over the period of study (overall straight-line displacement/sum daily movements; %)	13.7	8.9	26.8
Straight-line displacement between early and late March (24 nights; m)	1.66	47.55	–
Straight-line displacement between late March and late May (63 nights; m)	31.6	–	–
Straight-line displacement between late May and late December (216 nights)	–	–	–

Table 5. Above-ground movements by spool tracked snails (summed for three snails)

Object climbed	No. times recorded	Average height (cm)	Maximum height (cm)	Proportion of total movement by snails (%)
Over or along mossy fallen logs	15	29	58	8.0
Up base of tree trunks	6	24	42	1.0
Over surface tree roots and prostrate lianas	6	14	20	0.5
Over sticks and other debris	6	16	26	0.7

period (indicating the degree to which a single straight-line measurement between the start and end of the study period reflected actual movements) was more variable, ranging from 8.9% (snail 3) to 26.8% (snail 4). The measurements of straight-line displacement for animals relocated subsequent to the spool tracking study are also summarised in Table 4 and can be seen to also be highly variable. The final known location of both snails relocated was outside the immediate study area.

The majority of movement recorded during the spool tracking study was on the ground. Of the total distance traced (three snails pooled), 89.8% was on the forest floor. Above-ground movements (climbing) by the spool tracked snails were rare and generally of limited extent. Vertical movements were recorded on a total of 33 occasions (three snails pooled; Table 5). These movements usually comprised snails climbing over low obstructions, such as fallen logs and other debris, although on a few occasions snails were recorded climbing short distances up tree and sapling trunks. The greatest height above the ground recorded for a snail was 58 cm on a mossy fallen log and the longest single above-ground movement recorded was 9.10 m along the length of a mossy fallen log.

Table 6. Diurnal shelter sites of spool tracked snails (summed for three snails)

Location of shelter	No. times recorded	Proportion of total (%)
In open (>2 m from logs or trees)	17	46
Against logs (within 10 cm of log)	9	24
Near logs (within 25–50 cm of log)	6	16
Base of trees (within 20 cm of tree trunk or between buttress roots)	4	11
On logs	1	3
Total	37	100

Diurnal shelter sites

The locations of diurnal shelter sites recorded over the course of the study are shown in Fig. 3. No spool tracked snails were recorded returning to previously used shelter sites. A total of 37 different diurnal shelter locations were recorded for the three tracked snails (Table 6), some of which were occupied for 2 or more consecutive days during periods of nil overnight movement. Almost half the recorded sites were on the open forest floor. All shelter sites but one were on the ground, the exception being a site on top of a large mossy log. At all 37 diurnal sites spool tracked snails were found partially or fully buried in leaf litter.

Snails 5 and 6 were recorded opportunistically when they were found with or near spool tracked snails. Snail 5 was observed only on a single day (Day 7), when it was found sheltering on the ground surface hidden in the space under a slab of fallen wood. Snail 5 had moved away from this site on the following day and, although the site was checked several times throughout the remainder of the study, it was not found there again. Snail 6 was observed with one of the spool tracked snails (snail 3) partially buried in leaf litter on the open forest floor on Day 13. It remained here for two more nights (as described under breeding observations below) and then moved to a new site against a fallen log, after which it was not recorded again. Whereas the two diurnal shelter sites recorded for snail 6 were consistent with those recorded for the spool tracked snails, it is of note that the diurnal shelter site where snail 5 was found (a hidden cavity under fallen timber) was of a type not recorded for any of the spool tracked animals.

Breeding observations

Two egg-laying events were observed during the course of the study. Observations concerning these events are documented below. Table 7 provides a summary of breeding information for *H. falconeri* based on an amalgamation of the two observed events.

Breeding event 1

On Day 5 of the spool tracking study (mid-February), snail 2 was found partly buried under leaf litter close up against the side of a mossy fallen log. It remained here without moving for the next 4 nights and days. After it had moved away on the fifth night, the site was inspected and a clutch of 16 creamy white, rubbery shelled subspherical eggs were noted. The eggs were in a mass in a 5 cm deep, 8 × 4 cm wide hole in the soil below the leaf litter and were covered by leaf litter. The weight of the entire clutch of eggs was 35.5 g, which comprised 30.0% of the bodyweight of the snail at the start of the study. The average size of the eggs, based on measurement of a random sample of five eggs, was 18.8 × 16.4 mm and the average weight 2.2 g. The eggs swelled slightly over the next few days to become turgid creamy white spheres.

Table 7. Summary of breeding information for *Hedleyella falconeri*

Egg laying season:	mid to late February
No. eggs laid:	11–16 eggs laid over 3–5 nights
Egg size and weight:	mean size 18.3 × 15.7 mm; mean weight 2.1 g
Relative clutch mass:	30.0% of original bodyweight
Nest site:	4–5 cm deep hole in soil below leaf litter, close against fallen log or on open forest floor
Incubation period:	eggs hatch between 40 and 46 days
Shell size at hatching:	mean 14.9 mm high × 11.9 mm wide
Shell size at 145 days old:	mean 21.8 mm high × 15.1 mm wide
Shell size at 200 days old:	mean 22.3 mm high × 18.5 mm wide

The nest site was examined again in early April (46 days after egg laying finished) and the eggs were found to have hatched. Three live hatchling snails and one empty hatchling snail shell were observed within the nest site. The average hatchling shell size, based on the four shells noted, was 14.9 mm high by 11.9 mm wide. Hatchling shell shape was similar to that of adult *H. falconeri.*

Breeding event 2

On Day 13 of the spool tracking study (late February), snail 3 was found next to a new snail (snail 6), partly buried under leaf litter on the open forest floor. Both snails were situated side by side with the front end of the shell over a shallow 4 cm deep depression in the soil. Snail 3 was retracted entirely within the shell, whereas the body of snail 6 was partly extruded into the depression. Interpretation of the spool trail indicated that snail 3 had climbed onto and over snail 6 during the previous night.

On the following morning (Day 14), snail 3 had moved away but snail 6 had not moved and remained partially covered by leaf litter, with the front of the shell down in the shallow depression. Four creamy white, rubbery shelled eggs had been deposited in the deepest part of the depression over the previous 24 h. Snail 6 was still at the nest site on Day 15, when a total of eight eggs was counted. On Day 16, snail 6 had moved away from the nest site and a total of 11 eggs was counted in the nest. The eggs were in a 5 × 5 cm wide mass in a 4 cm deep hole in the soil below the leaf litter and were partly covered by the leaf litter (Fig. 4). The weight of the entire clutch of eggs was 22.5 g, giving an average egg weight of 2.0 g. The average size of the eggs, based on measurement of a random sample of five eggs, was 17.8 × 15.0 mm (Fig. 5).

In early April (39 days after egg-laying finished), the nest site was examined again and the eggs were noted to be close to hatching, with shelled snails clearly visible inside the transparent eggshells. Six eggs were collected and retained in captivity and hatched over the next few days. By early September (approximately 145 days after hatching), the average size of these snails was 21.8 mm high by 15.1 mm wide and by late October (approximately 200 days after hatching) the average size was 22.3 mm high by 18.5 mm wide.

Two hatchling snails and one intact egg were lodged in the Queensland Museum Malacology collection (specimen no. 67294).

Foraging observations

On two occasions, interpretation of spool tracks indicated that the snails had been feeding on fruiting bodies of the fungus *Polyporus varius* (Order Aphyllophorales) during nocturnal movements. Snails were usually retracted inside the shell when observed during

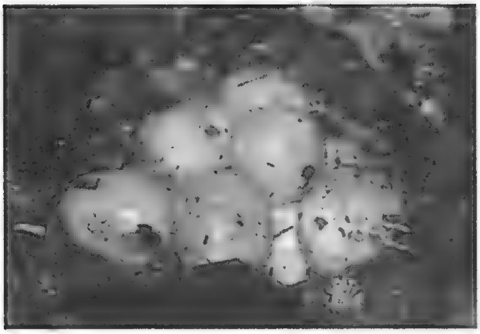

Fig. 4. Nest site of *Hedleyella falconeri* with the covering of leaf litter removed. The eggs were laid over a period of several days in a small hollow in the soil beneath the leaf litter.

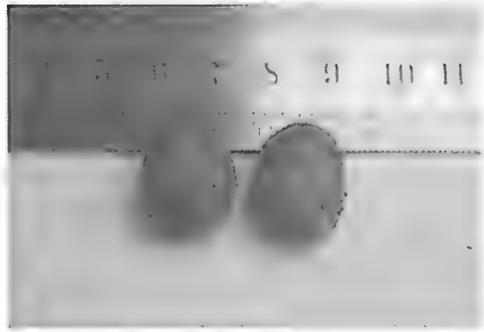

Fig. 5. Size of *Hedleyella falconeri* eggs. The large eggs each weighed approximately 2 g.

the day. However, on two occasions (separate to breeding observations), snails were found with their bodies partly extruded into the leaf litter beneath the shell and may have been feeding on rotting leaf litter material during diurnal resting.

Discussion

The present study is the first investigation of spatial and temporal patterns of habitat usage in an Australian land snail species that documents detailed quantitative and qualitative information at the scale of individual animals. Whereas the number of animals examined in this pilot study was low and caution needs to be exercised in extrapolation of the results, the findings have provided an increased understanding of the biology and ecology of *H. falconeri*. This is one of the first studies where the spool-and-line tracking technique has been applied to land snails. The first reported use of the spool-and-line technique in behavioural study of land snails was by Pearce (1990), comparing movement patterns and interactions between three North American land snail species. Other studies of movement patterns of land snails have typically relied on mark/recapture (Baker 1988; Baur and Baur 1988, 1990, 1992; Staikou *et al.* 1989; Cavagnaro *et al.* 2000). Time lapse cinephotography (Cook 1980; Bailey 1989), radiotracking (Tomiyama and Nakane 1993) and continuous observation (Cook 1979) have also occasionally been used. Both Pearce (1990) and the present study have demonstrated the significant value of the spool-and-line technique in ecological study of land snails.

Movement patterns and diurnal shelter sites

The results presented in this study concerning general activity patterns in *H. falconeri* supported a number of earlier observations of this species. Snails were found to be only nocturnally active, as previously noted by Jahnsen (1967), Shea (1978) and Bishop (1981), and were more likely to be active and to move greater distances on rainy nights than dry nights, consistent with earlier comments by Jahnsen (1967). McMichael and Iredale (1959) reported that, in general, the large land snail species from eastern Australian rainforests are very sensitive to dry conditions, appearing only at night and after rain and hiding away in moist places at other times. Similar correlation of activity with humid conditions or darkness has been reported in many other land snail species, including the European species *Helix aspersa* and *Helix lucorum* (Helicidae) (Bailey and Lazaridou-Dimitriadou 1986; Bailey 1989; Staikou *et al.* 1989) and the giant African snail *Achatina fulica* (Achatinidae)

(Tomiyama and Nakane 1993). It is likely to be a general behavioural pattern in many land snail species, assisting to minimise evaporative loss of body fluids and to reduce the high cost (Copley 2000) of mucous trail production. Many gardeners would probably attest to the veracity of the correlation between snail activity and wet nights.

Bishop's (1981) description of *H. falconeri* as a ground living species not climbing more than 0.5 m was also supported by the present study, with almost 90% of all movement recorded over the course of the study occurring on the ground surface and most climbing limited to passage over low obstacles, such as tree roots and fallen logs. Unlike sympatric land snail and slug species, such as *Thersites novaehollandiae* (Camaenidae) and *Triboniophorus graeffei* (Athoracophoridae), which can often be observed at moderate to high heights on tree trunks as well as on the ground (personal observations), *H. falconeri* does not appear to forage or shelter in trees.

The only previous reference to distances moved by *H. falconeri* is a single record, based on following a slime trail, of a juvenile snail (shell width 5 cm) moving a distance of approximately 30 m over an unknown time period (Jahnsen 1967). In the present study, *H. falconeri* moved an average of almost 9 m per night on the nights when it was active, with a maximum of over 21 m in a single night. Much of this movement (up to 45%) was meandering, but still resulted in straight-line displacement of up to 25.5 m over 16 nights and 47.55 m over 24 nights. It is evident that *H. falconeri* has considerable dispersal capacity provided there is continuity of habitat. Baur and Baur (1990) found that an 8 m wide paved road with low traffic density and, to a lesser extent, a 3 m wide unpaved track were sufficient to form a significant dispersal barrier for the European land snail *Arianta arbustorum* (Helicidae). However, movement in *A. arbustorum* (shell diameter 16–22 mm) averages only 0.58 m per day, with a maximum of up to approximately 4.4 m per day (Baur and Baur 1992), substantially less than that recorded for *H. falconeri* in the present study, and it is anticipated that greater barriers (e.g. wider or busier roads) would be needed to significantly obstruct movement and isolate populations of *H. falconeri*.

Comparison with other land snail species indicates that daily distances moved by *H. falconeri* are generally relatively large, probably reflecting, in part, its greater body size. Baur and Baur (1988) reported that the tiny European land snail *Punctum pygmaeum* (Endodontidae) (shell diameter 1–1.5 mm) had an average displacement of only 47 mm per 12 h. *Cernuella virgata* (Helicidae) (shell diameter 10–15 mm) was found to move on average between 0.1 and 0.4 m per day (Baker 1988). Pearce (1990), spool tracking three different land snail species with shell sizes of 15–25 mm diameter, recorded average daily movements of 0.76 to 2.25 m per day. Daily movements of an extent similar to *H. falconeri* were recorded in juveniles of the large land snail species *A. fulica* (shell length 50–57 mm), averaging between 5 and 9 m per day (Tomiyama and Nakane 1993).

Some earlier reports suggested that *H. falconeri* actively selected particular types of sites for diurnal shelter. Jahnsen (1967) suggested that the selection of secure diurnal shelter sites was essential for *H. falconeri* to avoid predation by diurnal ground foraging rainforest birds and reported finding snails sheltering under large rocks and slabs of fallen timber. Bishop (1981) reported that *H. falconeri* preferred diurnal shelter sites among the twisted roots of strangler fig trees, implying a high degree of active site selection. The results presented here do not support the notion of active and frequent selection of secure diurnal shelter sites. Almost half the shelter sites recorded in the present study simply comprised partial or complete burial under leaf litter on the open forest floor and the remainder were merely close to or up against the sides of logs or tree bases. None of the spool tracked snails was recorded using shelter sites that would be

secure against diurnal predators, despite the availability in the study area of a fig tree with suitable crevices and root spaces at ground level and an abundance of fallen logs and pieces of timber, as well as the presence in the study area of the noisy pitta (a known predator) and other likely diurnal predators, including the superb lyrebird *Menura novaehollandiae* (Menuridae) and Australian brush turkey *Alectura lathami* (Megapodidae). Nevertheless, the three tracked snails all successfully avoided predation during the 17 day duration of the spool tracking study, with at least two of the three surviving a further 24 days following the end of the tracking study and at least one surviving a further 87 days. It is not known whether the other snails not relocated in these later searches were alive but not found or had been predated, but the fact that the last known site of the two relocated snails was outside the original study area suggests it is quite likely they were simply beyond the area searched.

One of the additional *H. falconeri* found and marked during this study (snail 5) was found in a secure diurnal shelter site under a slab of fallen timber, although it was not found there again during the remainder of the study. The author has previously found *H. falconeri* by day in similar sites on numerous occasions. This study, however, suggests that such secure shelter sites are not actively sought for every night by *H. falconeri*, but are simply used as they are randomly encountered and are not consistently re-used once found. Previous conclusions regarding the significant use of secure diurnal shelter sites, such as under logs and rocks, may be the result of paradigm based search pattern biases of the researcher rather than a true pattern of the snail. Certainly, the species is more abundant when observed at night than one would surmise based on diurnal searches (Bishop 1981; personal observations).

As noted above, all the diurnal shelter sites recorded in this spool tracking study involved partial or complete burial under leaf litter. Sheltering under leaf litter probably serves the dual function of providing a moist refuge and a degree of concealment from diurnal predators. Evidently simply hiding below leaf litter on the open forest floor is sufficient for *H. falconeri* to usually evade diurnal snail researchers, although concealment from diurnal predators is obviously not absolute, because *H. falconeri* is a common prey item of the noisy pitta.

The present study recorded no instances of return to and re-use of shelter sites once snails had moved away. Even the non-tracked snail found in a secure site under a fallen piece of timber was not found there again on subsequent inspections. This, together with the observation that the two marked snails relocated after the end of the spool tracking study had both moved beyond the original study area, suggests that *H. falconeri* does not occupy a home range, but is nomadic, moving randomly around the forest floor and sheltering wherever it finds itself at the end of the night. Jahnsen's (1967) description of two *H. falconeri* found by day retracted inside their shells in the middle of a bush road, having failed to completely cross during the previous night, is consistent with the type of behaviour observed in the present study. Pearce (1990) found a similar result spool tracking three North American land snail species, with snails re-using refuges only occasionally. Baur and Baur (1992) also found no evidence of homing behaviour in *A. arbustorum*, snails showing no preference in direction of movement, with directions chosen on consecutive days being independent from each other.

The apparently nomadic behaviour observed in the present study contrasts with studies of some other land snail species, which have reported homing behaviour and re-use of diurnal shelter sites (Edelstam and Palmer 1950; McLauchlan 1951; Cook 1980). Staikou *et al.* (1989) suggested that homing behaviour may be more advantageous

in open habitats, where temperature and evaporation rates are more extreme, than in the favourable environments provided in well vegetated habitats. Therefore, the nomadism of *H. falconeri* may be a reflection of the equable environment for land snails in subtropical rainforest.

Nomadism and homing to a precise site represent the two end-points of a spectrum of possible movement behaviours for land snails. Examples of intermediary behaviours include *H. aspersa*, which Bailey (1989) reported as tending to choose particular areas for roosting but rarely returning to the exact same spot, and *A. fulica*, in which older adults maintain discrete home ranges but within which diurnal resting sites are not fixed (Tomiyama and Nakane 1993).

Some studies have reported seasonal or other longer scale homing or directional movement behaviour in some land snail species. McLauchlan (1949) reported *Strangesta capillacea* (Rhytididae) in an urban garden environment moving around in relatively open areas during periods of wet weather of up to 3 weeks duration, returning again to shelter in moist, sheltered refuge areas during intervening dry conditions. Baker (1988) recorded directional seasonal movement between pasture and roadside vegetation by *C. virgata*. Bailey (1989), citing references to seasonal migration of *Helix pomatia* (Helicidae) to traditional shelter sites, suggested that choice of a traditional shelter site may be more advantageous than on-the-spot assessment, particularly if the selection had to be made before the conditions that made the site suitable became apparent. The present study extended over only 17 nights and did not investigate seasonal scale differences or longer term patterns in movement by *H. falconeri*. Further study would be required to identify whether any longer term patterns exist in this species.

Size or age related differences in movement patterns have been reported in some land snail species. Baur and Baur (1988), for example, found a positive correlation between shell size and average displacement in *P. pygmaeum*. In contrast, Tomiyama and Nakane (1993) found a negative correlation between age and average dispersal distance in *A. fulica*, with juveniles being significant dispersers and young adults having continuously shifting home ranges, whereas older adults maintained a more restricted and constant home range. Baur and Baur (1989) found no age related correlation in *A. arbustorum*. These different patterns (or lack of pattern) probably reflect different life history strategies between different land snail species. Tomiyama and Nakane (1993), for example, proposed that the negative correlation found in *A. fulica* was related to its protandrous maturation, allowing younger sperm producing adults to increase their reproductive fitness by searching widely for older egg producing adults. Further study with a greater sample size including a range of age classes would be necessary to determine whether any age related movement patterns exist in *H. falconeri*.

Breeding observations

The observations of egg laying in *H. falconeri* made during the present study were an unexpected bonus and illustrate the value of close observation of natural behaviour required in such studies. The descriptions of egg size, clutch size and nest site for *H. falconeri* presented here are consistent with those provided by Jahnsen (1967), who maintained the species in captivity and described two separate clutches of marble sized (15 mm diameter) white eggs, one of 14 eggs and the other of 16 eggs, both deposited in small depressions in the soil and then covered with debris to a depth of approximately 2.5 cm. Jahnsen (1967) recorded *H. falconeri* eggs in December and January, 1–2 months earlier than the present study, and also reported observing *H. falconeri* mating in September. Information detailed

in the present study concerning relative clutch mass, time taken to lay eggs, incubation period, hatchling size and early growth rate details has not previously been described for *H. falconeri*.

Unfortunately, little information is available to enable comparison of reproductive details in *H. falconeri* with other Australian land snail species (Bishop 1981). Smith (1992) noted that large eggs were typical of many caryodid land snail species. Hedley (1892) reported that *Pygmipanda atomata* (Caryodidae) laid large white hard-shelled eggs. Jahnsen (1967), who maintained *P. atomata* in captivity, provided further details, including that egg size was approximately 5 mm in diameter, clutch size between 13 and 20 eggs, laying occurred in November and December, the nest site comprised a small cavity in the soil under leaf litter and eggs hatched in approximately 32 days, with progressive hatching of eggs, a few per day, presumably reflecting laying over several days. Similarities between *P. atomata* and *H. falconeri* in addition to the large egg size include approximate clutch size, nest site and probably egg laying extending over several days.

The nest sites recorded in the present study were not in secure locations, such as under fallen logs, and would be vulnerable to predation by ground litter foraging birds. However, there was no indication of the eggs apparent from the surface of the leaf litter at the two nest sites recorded and it is probable that discovery of nest sites by predators, such as birds, relies on random chance, with sufficient nest sites escaping discovery to maintain population levels.

Feasibility and value of the spool-and-line tracking technique

The spool-and-line tracking technique was found to work well for field study of *H. falconeri*. The spools were very easy to affix to the hard dry shell surface, stayed firmly in place for the duration of the study and, attached to the rear of the shell, did not appear to impede movement of the animals. Distances moved by *H. falconeri* were such that a single spool per animal was amply sufficient for the duration of the present study and, in fact, would probably have sufficed for at least 25 days. *Hedleyella falconeri* was sufficiently large to ensure that the 5 g spool mass used in the present study did not exceed the recommended level of 10% of the subject animal's body mass for tracking devices on small animals (Richards *et al.* 1994). Lighter spools are available that would be suitable for use on medium sized land snail species. Pearce (1990) used a modified spool measuring only approximately 25 mm by 6–8 mm and weighing less than 1 g on land snails with a shell diameter of 15–25 mm.

As discussed above, the application of the spool tracking technique enabled the collection of detailed quantitative and qualitative data for several aspects of ecology and biology that would otherwise be difficult to study in the field. Direct monitoring of snail movements in natural habitats is difficult, with observation related disturbance potentially altering the snails' behaviour (Baur and Baur 1990). Furthermore, the most mobile individuals that leave the search area and the least mobile individuals that remain hidden are likely to be underrepresented in mark/recapture sampling (Baur and Baur 1990). The spool tracking technique enabled continuous and detailed monitoring of movement by an indirect means, thereby minimising observation-related disturbance, and allowed animals to be relocated regardless of distance moved, avoiding sampling biases. Comparison of spool trail length and straight-line displacements in the present study (on both a daily basis and over the course of the study) demonstrated the significant degree to which movement studies based on point locations, such as mark/recapture or radiotracking studies, can underestimate actual distances moved. It is considered that the cheap, simple and effective

spool-and-line technique has great potential in the study of medium to large land snail species and can provide much information concerning their behaviour and ecology to assist with their conservation.

Conservation implications and conclusions

This study indicated that *H. falconeri* is reliant on the leaf litter layer on the rainforest floor for foraging, shelter and breeding. Degradation or loss of this key habitat component through impacts such as fire, intensive forestry or grazing by domestic stock is likely to significantly and adversely affect the species. *Hedleyella falconeri* does not appear to rely on known or traditional diurnal shelter sites, but gambles on finding suitable shelter wherever its nomadic movements lead it. On the one hand, this nomadism, together with the distances the species is able to cover, provides a relatively high dispersal capacity, so that recolonisation of regenerating habitat is likely if populations survive nearby. On the other, it is a strategy that works well in the highly favourable conditions for land snails provided by eastern Australian rainforests, but is reliant on the continued conservation of those rainforest habitats.

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Some Recent scissurellids from the New Zealand region and remarks on some scissurellid genus group names (Mollusca : Gastropoda : Vetigastropoda)

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Abstract

Taxonomic problems relating to interpretations of type species of *Scissurella* d'Orbigny, 1824, *Schismope* Jeffreys, 1856, *Woodwardia* Crosse & Fischer, 1861 and *Sinezona* Finlay, 1926 are discussed. *Daizona* Bandel, 1998 is interpreted as a synonym of *Sinezona*. *Ariella campbelli* Bandel, 1998 and *Sinezona pacifica* Bandel, 1998 are relegated to synonymy under *Sinezona levigata* (Iredale, 1908) and *Sinezona pacifica* (Oliver, 1915) respectively; *Scissurella stellae* Fleming, 1948 is synonymised with *Scissurella prendrevillei* Powell, 1933; and *Scissurella prendrevillei*, *Scissurella fairchildi* Powell, 1933, and *Scissurella marshalli* Bandel, 1998 are contrasted. A new species of *Sinezona* from north-eastern New Zealand is described and a neotype is designated for *Sinezona pacifica* (Oliver, 1915). *Scissurella mantelli* Woodward, 1859 is shown to have been consistently misidentified and the New Zealand species hitherto so identified is described as a new species of *Thieleella* Bandel, 1998. Three additional recent misidentifications of taxa from the New Zealand region are also indicated.

Additional keywords: *Anatoma*, distribution, new synonyms, new taxa, *Schismope*, *Scissurella*, Scissurellidae, *Sinezona*, *Thieleella*, *Woodwardia*.

Introduction

Among the small marine snails of the family Scissurellidae recently described and illustrated by Bandel (1998) were three new species group taxa and two previously named taxa from the New Zealand region, and a record of *Larochea miranda* Finlay, 1927 from Queensland. The primary objectives of the present contribution are to indicate that two of these three new taxa are junior synonyms, that the others are misidentified, and to discuss taxonomic problems relating to interpretation of *Scissurella* d'Orbigny, 1824, *Schismope* Jeffreys, 1856, *Woodwardia* Crosse & Fischer, 1861 and *Sinezona* Finlay, 1926. The opportunity is taken to indicate that *Scissurella stellae* Fleming, 1948 is a junior synonym of *S. prendrevillei* Powell, 1933 and to provide a replacement name for the New Zealand species currently known as *Anatoma mantelli* (Woodward, 1859), which is based on misinterpreted and mislocalised type material.

The New Zealand scissurellid fauna includes type species of five genus-group taxa and is particularly rich, with 22 named species (all of which are restricted endemics) plus approximately the same number of undescribed species (material NMNZ). This total excludes taxa newly synonymised herein and *Sinezona subantarctica* (Hedley, 1916), an endemic restricted to Macquarie Island (politically Australian), which has been included in the New Zealand fauna (Powell 1979).

Materials and methods

Unless specified, all material is held at the Museum of New Zealand Te Papa Tongarewa (NMNZ; registration numbers are preceded by 'M.').

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Abbreviations and text conventions

AMS	Australian Museum, Sydney.
CM	Canterbury Museum, Christchurch.
LACM	Los Angeles County Museum of Natural History.
NZGS	Institute of Geological and Nuclear Sciences, Lower Hutt.
NMNZ	Museum of New Zealand Te Papa Tongarewa, Wellington.

Systematics

Superfamily **SCISSURELLOIDEA** Gray, 1847

Family **SCISSURELLIDAE** Gray, 1847

Remarks

Uncertainty has long persisted as to the identity of some European scissurellids, primarily because type material is apparently no longer extant. Key taxa are *Scissurella laevigata* d'Orbigny, 1824, *S. elegans* d'Orbigny, 1824, *S. costata* d'Orbigny, 1824, *S. striatula* Philippi, 1844 and *S. cingulata* O. G. Costa, 1861. Even if type material is indeed lost, at least some of these well-known names could be conserved and stabilised by designation of neotypes (ICZN 1999), ideally illustrated by scanning electron micrographs and with due consideration to the taxonomic problems involved (see below). As a case in point, Burnay and Rolan (1990) interpreted *S. cingulata* as a *nomen dubium* because type material is apparently lost and because the description and original illustration (Costa 1861) are somewhat ambiguous. Fortunately, their opinion has not been widely accepted. A far better course of action would be to conserve the name for the common Mediterranean species to which it is usually applied (e.g. Sabelli *et al.* 1990, 1992; Giannuzzi-Savelli *et al.* 1994), based on a neotype from Sardinia, the type locality.

Subfamily **SCISSURELLINAE** Gray, 1847

Genus ***Scissurella*** d'Orbigny, 1824

Scissurella d'Orbigny, 1824: 343. Type species (by subsequent designation of Gray, 1847: 146): *Scissurella laevigata* d'Orbigny, 1824 (= ? *S. costata* d'Orbigny, 1824); Recent, Mediterranean.

Schismope Jeffreys, 1856*a*: 321. Type species (by monotypy): '*Scissurella striatula* Philippi, 1844' (misidentified).

Woodwardia Crosse & Fischer, 1861*a*: 160. Type species (by monotypy): '*Scissurella elegans* d'Orbigny, 1824' (misidentified).

Remarks

The New Zealand species referred to *Scissurella* below differ from such apparently typical *Scissurella* species as *S. costata* in details of protoconch sculpture, including stronger axial ribs that occupy only the outer half of the exposed part of the protoconch, the lack of an irregular network of threads at the tip of the apical fold and a spiral thread, and in that the terminal varix is not attached to the tip of the apical fold. Evaluation of the significance of these differences is beyond the intention of the present article.

Wenz (1938), followed by Bandel (1998), cited *S. costata* d'Orbigny, 1824, as a type species of *Scissurella*, presumably on the assumption that *S. laevigata* d'Orbigny, 1824 was a synonym of *S. costata*. However, this synonymy remains to be demonstrated convincingly.

Jeffreys (1856*a*) introduced *Schismope* with the following comments:

> 'The slit in *S. striatula*, Ph., does not commence until the animal is half grown. Its sides or walls are raised above the surface of the shell, and present a prominent ridge ... the foramen in which it terminates is oblong-fusiform ... The foraminal termination of the slit I have only observed in this species ...'

Jeffreys's description is accordant with the Mediterranean species normally identified as *Sinezona cingulata* (O. G. Costa, 1861), which is currently grouped in *Sinezona* (e.g. Sabelli *et al.* 1990; Giannuzzi-Savelli *et al.* 1994). However, judging from Philippi's (1844, pl. 25, fig. 33) illustration, *Scissurella striatula* has an entirely different shell with a tiny spire, a flat sutural ramp, a large umbilicus, a pronounced shoulder angulation surmounted by a long selenizone and an open slit. Thus, *Schismope* is based on a misidentified type species. Note that Anistratenko and Starobogatov (1997) have proposed a neotype for *Scissurella striatula*, which they refer to *Anatoma* Woodward, 1859 (type species *Scissurella crispata* Fleming, 1828) and consider specifically distinct from *Scissurella laevigata* (? = *S. costata* d'Orbigny, 1824), with which it has sometimes been associated (e.g. Sabelli *et al.* 1990).

Crosse and Fischer (1861*a*) introduced *Woodwardia* for *Scissurella elegans* d'Orbigny, 1824 alone, diagnosing the new genus thus: 'Testa juvenis apertura integra, major fissura marginali, adulta formine munita, margine integro'. Their concept of *S. elegans* was based on illustrations of specimens so identified by Woodward (1859), which appear to represent the *Sinezona* species normally identified as *S. cingulata*. Woodward evidently considered that d'Orbigny's (1824) figured specimen of *S. elegans* was subadult because it has a selenizone that terminates in an open slit. Although d'Orbigny depicted a shell with a selenizone much longer than any known species of *Sinezona*, the illustration is certainly inaccurate and misleading because no known scissurellid has a selenizone that commences so early on the teleoconch. Nevertheless, the illustration of *S. elegans* is certainly far more like *Scissurella costata* than *Sinezona cingulata* and, thus, seems more likely to represent a species of *Scissurella* than *Sinezona*. Regrettably, type material of *S. elegans* appears to be no longer extant and, without topotypes (from the Piacentian, Upper Pliocene, of Castell'Arquato, Italy), it is impossible to deduce the affinities of the species with any certainty. Whatever the case, it seems clear that *Woodwardia* is also based on a misidentified type species. Crosse and Fischer (1861*b*) eventually realised that Jeffreys had introduced *Schismope* for the same group and synonymised *Woodwardia* with *Schismope*.

Short of petitioning the International Commission on Zoological Nomenclature, ideally for suppression of *Schismope* and *Woodwardia* (which seems unnecessary), the most obvious and least disruptive course of action is to maintain predominant current usage by interpreting their type species as specifically indeterminable members of the genus *Scissurella*, in which case both fall as synonyms of *Scissurella* (e.g. Keen 1960; Abbott 1974; Herbert 1986; Sabelli *et al.* 1992).

Bandel (1998), evidently unaware of these problems, used *Schismope* (with *Scissurella cingulata* as 'type species') for species here referred to *Sinezona* (see below).

Of historical interest is the extraordinary and acrimonious exchange between Jeffreys and Woodward that followed introduction of *Schismope* (Jeffreys 1856*b*,*c*; Woodward 1856*a*,*b*).

Scissurella fairchildi Powell, 1933

(Figs 1–3)

Scissurella fairchildi Powell, 1933*a*: 34, pl. 6, figs 3, 4; Powell, 1979: 34, pl. 13, figs 16, 17.

Material examined

Holotype. Off Bounty Islands, New Zealand, 311 m; CM M5316.

Other material examined. Proclamation Island, Bounty Islands, 47°42′S, 179°05′E, 39 m (24, M.119755); off Bounty Islands, 91 m (4, M.91946); NW point of Leeward Island, Antipodes Islands, 13 m (1, M.152618); off Antipodes Islands, 49°40.19′S, 178°44.30′E, 113 m (many, M.150149).

Distribution

Antipodes and Bounty islands, New Zealand, 39–311 m (shells only).

Remarks

Scissurella prendrevillei (see below) is a distinct allopatric species that is more widely distributed off southern New Zealand.

Scissurella prendrevillei Powell, 1933

(Figs 4–6)

Scissurella, n. sp. Finlay, 1928: 234.
Scissurella prendrevillei Powell, 1933*b*: 193, pl. 33, fig. 6; Powell, 1979: 34, pl. 13, fig. 14.
Scissurella stellae Fleming, 1948: 84, pl. 6, fig. 3, pl. 8, fig. 4; Powell, 1979: 34. **New synonymy**.

Material examined

Holotype, Scissurella prendrevillei. Off Owenga Beach, Chatham Islands, New Zealand, 18 m, Auckland Institute and Museum No. 70701.

Holotype, Scissurella stellae. Northport, Chalky Sound, Fiordland, New Zealand, 13 m, NZGS TM421.

Other material examined. Fossil: Ohope, shellbeds and blue muddy siltstone below old reservoir in stream foot of Ohope–Whakatane road (W15/644519), Late Pleistocene (Castlecliffian), M.150234 (1); Te Piki road cutting, between Whangaparaoa and Te Araroa (Y14/561904), Holocene (Haweran) (7, M.40192; 1, M.150153). Recent: several thousand specimens (153 lots, NMNZ) from throughout the geographic and bathymetric range.

Distribution

Late Pleistocene to Recent. Three Kings, North, South, Stewart and Chatham Islands, New Zealand, 0–805 m; taken alive at 9–163 m from bryozoan/shell substrata (common).

Remarks

From direct comparison of type material and scanning electron micrographs of topotypes, *Scissurella stellae* Fleming, 1948 is indistinguishable from the prior *S. prendrevillei* Powell, 1933. *Scissurella prendrevillei* differs from *S. fairchildi* in having fewer and stronger axial costae on the teleoconch, in the later appearance of the selenizone and in details of protoconch sculpture. An undescribed species with finer, more numerous axial costae than in *S. fairchildi*, *S. prendrevillei* and *S. marshalli* occurs with the latter two species off the far northern North Island and the Three Kings Islands (e.g. M.148569).

Scissurella marshalli Bandel, 1998

(Figs 7–9)

Scissurella marshalli Bandel, 1998: 12, pl. 2, fig. 4–6.

Material examined

Holotype. Reef between Great Island and Farmer Rocks, Three Kings Islands, New Zealand, 34°09′S, 172°10′E, 33 m, 17 Feb. 1986, scuba, G. S. Hardy, NMNZ M.93992.

Other material examined. Several hundred specimens (21 lots NMNZ).

Distribution

Off Three Kings Islands, New Zealand, 33–805 m, from comminuted bryozoan/shell substrata (shells only).

Remarks

Scissurella marshalli differs from *S. prendrevillei* in attaining a smaller size, in the earlier appearance of the selenizone, in the more strongly produced rim at the start of the selenizone, in that the axial costae on the teleoconch weaken as they approach the suture and in details of protoconch sculpture.

Genus ***Sinezona*** Finlay, 1926

Sinezona Finlay, 1926: 341, 346. Type species (by original designation): *Schismope brevis* Hedley, 1904; Recent, New Zealand.

?*Coronadoa* Bartsch, 1946: 281. Type species (by original designation): *Coronadoa simonsae* Bartsch, 1946; Recent, California.

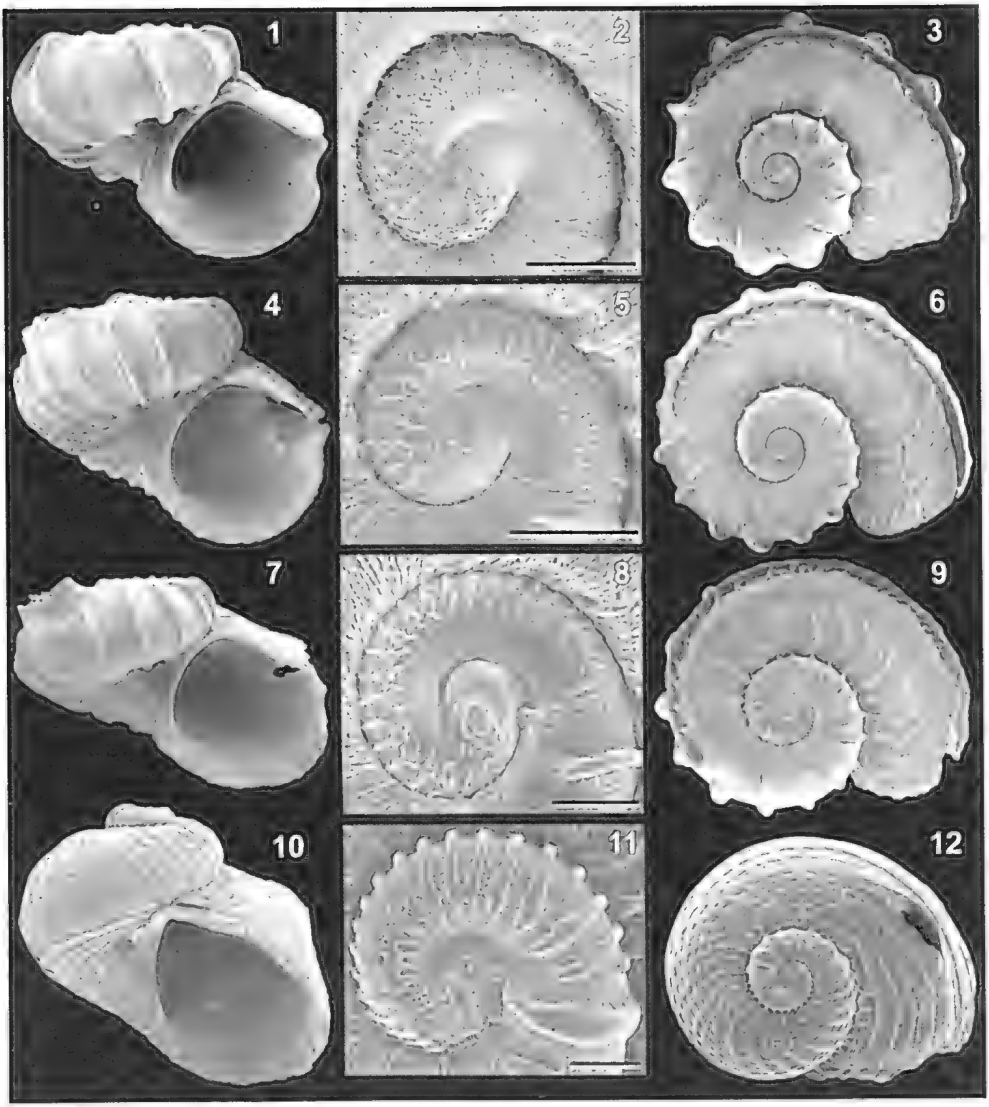
Daizona Bandel 1998: 57. Type species (by original designation): *Sinezona doliolum* Herbert, 1986; Recent, southern Africa. **New synonymy**.

Schismope of author, not Jeffreys, 1856 (based on misidentified type species).

Woodwardia of author, not Crosse & Fischer, 1861 (based on misidentified type species).

Remarks

As here limited, *Sinezona* comprises a group of species in which the protoconch is strongly axially ribbed (no spiral sculpture, no irregularly reticulate sculpture at the tip of the apical fold and terminal varix not connected to the tip of the apical fold) and the anal slit is closed behind the apertural rim to form a foramen at maturity. There is fluid transition in the degree of selenizone development between species in which the selenizone commences at the beginning of the last adult whorl and the terminal foramen either narrows and extends to the apertural rim as a slit (e.g. *S. doliolum* Herbert, 1986; Herbert 1986: fig. 31) or is closed anteriorly well before the outer lip (e.g. *S. pacifica* (Oliver, 1915) and *S. bandeli* new sp., figs 18, 21), through intermediate forms in which the selenizone commences before, at or after the middle of the last adult whorl and the foramen is closed anteriorly (e.g. *S. insignis* (E. A. Smith, 1910), *S. cingulata*, and *S. brevis* (Hedley, 1904: fig. 15)) to those in which the selenizone is very short or entirely absent (foramen only; e.g. *S. levigata* (Iredale, 1908: fig. 12) and *S. pauperata* Powell, 1933: Marshall 1993, fig. 1*A*). Contrary to the opinion of McLean (1967), *Coronadoa simonsae* Bartsch, 1946 is not based on juveniles of *S. rimuloides* (Carpenter, 1865), but appears to be a distinct, although otherwise similar, species of *Sinezona* that attains maturity without ever forming a trace of



Figs 1–12. Shells of *Scissurella* and *Sinezona* species. *1–3*, *Scissurella fairchildi* Powell, 1933, Proclamation Island, Bounty Islands, 39 m, M.119755 (width 1.05 mm). *4–6*, *Scissurella prendrevillei* Powell, 1933, off Bauza Island, Doubtful Sound entrance, 20 m, M.141663 (width 1.03 mm). *7–9*, *Scissurella marshalli* Bandel, 1998, off Three Kings Islands, 91 m, M.33651 (width 0.95 mm). *10–12*, *Sinezona levigata* (Iredale, 1908), off Five Fingers Peninsula, Fiordland, 37 m, M.144348 (width 1.00 mm). Scale bars: 50 μm.

either a selenizone or a foramen (material examined of both taxa collected living off Ben Rock, south of San Martin Island, Baja, California, 16–31 m, LACM 72–112).

Bandel (1998) proposed *Daizona* and *Ariella* (type species *Ariella haliotimorpha* Bandel, 1998; Oligocene, France) as genera for species with a long selenizone and none at all, respectively, and referred species with intermediate degrees of selenizone development to '*Schismope*' and *Sinezona*. As indicated above, conceptually, *Schismope* and *Woodwardia* are both based on a species (probably *S. cingulata*) with a selenizone of moderate length with an anteriorly closed terminal foramen, although their (misidentified) nominal type species belong in *Scissurella*.

Besides lacking a selenizone, the type species of *Ariella* is characterised by its extremely small size (shell width 0.50 mm). Bandel (1998) referred the New Zealand species *Sinezona pauperata* Powell, 1933 to *Ariella* because it is also very small and lacks a selenizone (it has far more numerous axial riblets on the protoconch than *A. haliotimorpha*). Bandel also referred *Sinezona subantarctica* (Hedley, 1916) and *Ariella campbelli* Bandel, 1998 (= *S. levigata*) to *Ariella*, although there can be little doubt that they belong in *Sinezona s. str.* (see below).

In view of the continuous interspecific gradation in selenizone length, and particularly the absence of supporting anatomical and radular data, it seems impossible to justify *Daizona*, so it is here interpreted as a synonym of *Sinezona*.

In proposing *Sinezona*, Finlay (1926) stated that 'The absence of the fasciole girdle suggests the name chosen for the genus ...', which is unfortunate given that the good original illustration of the type species (Hedley 1904, text fig. 16) clearly shows a selenizone of moderate length. On purely etymological grounds, Herbert (1986) suggested that *Sinezona* may be based on a misidentified type species. However, Finlay (1926: 341, 346) explicitly introduced *Sinezona* '... for the *Schismope brevis* group' (*S. brevis* unequivocally designated as type species by Finlay (1926: 346)), in which he included *S. levigata* and *S. subantarctica* (Hedley, 1916), the former having a very short selenizone and the latter none at all. Finlay's statement that *S. levigata* has a 'generally quite smooth' spire suggests that he wrote from memory, influenced by the inappropriate etymology, a contention supported by the statement (later in the same paragraph) that the finely reticulately sculptured species *S. subantarctica* '... differs from *S. levigata* in being smoother'. Finlay's concept of *S. levigata* was extremely unlikely to be based on specimens of *Incisura lytteltonensis* (E. A. Smith, 1894) or *Scissurona rosea* (Hedley, 1904; the only nominal, more or less smooth Recent scissurellids known from the New Zealand region) because the original illustrations of these common, highly distinctive species clearly show a slit extending to the apertural rim.

I have not explored the possibility that some *Sinezona* species may have a terminal slit that remains wide open to the apertural rim, as in *Scissurella*, but it seems possible that these may exist, given that the foramen extends to the apertural rim as a slit in *Sinezona doliolum* Herbert, 1986. Such species would presumably be distinguishable from *Scissurella* species on protoconch morphology, the latter typically having much finer axial sculpture, a spiral thread, an irregular network of threads at the tip of the apical fold and a terminal varix that is connected to the tip of the apical fold.

Sinezona levigata (Iredale, 1908)

(Figs 10–12)

Schismope brevis levigata Iredale, 1908: 381; Suter, 1913: 91.
Sinezona laevigata [sic]. Finlay, 1926: 341; Powell, 1955: 46.
Sinezona levigata. Powell, 1979: 35.
Sinezona brevis. Bandel, 1998: 61, pl. 21, figs 2–5 (not Hedley, 1904).
Ariella campbelli Bandel, 1998: 64, pl. 22, figs 5–7. **New synonymy.**

Type data

Schismope brevis levigata. Type material probably no longer extant; Sandfly Bay, Otago Peninsula, New Zealand.

Material examined

Holotype, Ariella campbelli. Campbell Island, New Zealand, AMS C.162251.
Other material examined. Several hundred specimens (72 lots NMNZ) from throughout the geographic and bathymetric range.

Distribution

Southern North Island, South, Stewart, Snares, Auckland, Campbell, Antipodes, Bounty and Chatham Islands, New Zealand, 0–113 m; taken alive intertidally to 10 m from algae.

Remarks

Ariella campbelli Bandel, 1998 is based on a Campbell Island specimen of *Sinezona levigata*, specimens of which were described and illustrated in the same publication (Bandel 1998: 61, pl. 21, figs 2–5) as *S. brevis* (M100499). *Sinezona levigata* is common and widely distributed in the southern part of the New Zealand region and occurs sympatrically with *S. brevis* off the southern North Island, the northern South Island and at the Chatham Islands. *Sinezona levigata* may be distinguished from *S. brevis* by shorter selenizone, larger aperture, closed instead of open umbilicus (occluded by spreading inner lip), a slightly more eccentric apex, lower axial riblets on the first half teleoconch whorl and uninterrupted and more crowded axial riblets on the last adult whorl.

There is considerable variation in degree of development of the selenizone, both within and between populations. In most specimens from Campbell Island, the Antipodes Islands and the Bounty Islands, the selenizone is typically extremely short or entirely absent and is up to 200 µm long in a few specimens. In samples from off the Snares Islands, the selenizone ranges from absent to 430 µm in length, whereas in samples from Fiordland the selenizone is typically less than 270 µm long. Whereas there is certainly a higher proportion of specimens without selenizones in populations from the extreme south, there is complete gradation between specimens in which the selenizone is well developed or absent in populations from the Snares Islands, Stewart Island and the southern South Island and there is no obvious north–south cline in selenizone length. Because there does not appear to be any difference associated with selenizone length, it is concluded that all the populations examined are conspecific.

Iredale (1908) stated that the type material of *S. levigata* was 'to be presented to the Canterbury Museum, Christchurch', but there is no evidence that it was ever received there (Freeman *et al.* 1997). Moreover, type material was not traced in any other New Zealand national collection (or AMS) and is probably no longer extant.

Sinezona brevis (Hedley, 1904)

(Figs 13–15)

Schismope brevis Hedley, 1904: 90, text fig. 16; Suter, 1913: 91, pl. 6, fig. 14.
Sinezona brevis. Finlay, 1926: 341; Keen, 1960: 221, fig. 136/2; Powell, 1979: 34, pl. 13, figs 10, 11.
Woodwardia (*Sinezona*) *brevis*. Wenz, 1938: 173, fig. 272.
Sinezona iota. Bandel, 1998: 62, pl. 21, figs 6–8 (not Finlay, 1926).
NOT *Sinezona brevis*. – Bandel, 1998: 61, pl. 21, figs 2–5 = *S. levigata* Iredale, 1908.

Material examined

Holotype. Lyall Bay, Wellington, New Zealand, AMS C.13591.

Other material examined. Several hundred specimens (49 lots NMNZ) from throughout the geographic and bathymetric range.

Distribution

Three Kings, North, northern South and Chatham Islands, New Zealand, 0–46 m; taken alive intertidally to 6 m from algae.

Remarks

Bandel (1998) described and illustrated a Chatham Islands specimen of *S. brevis* under the name *Sinezona iota* Finlay, 1926. *Sinezona iota* differs from *S. brevis* in attaining a smaller size, in being taller and narrower, in having a much longer selenizone and a longer slit and in that the axial ribs on the protoconch are absent from a broad inner zone and are strongly thickened and in contact with one another in a narrow zone at the summit. The species described and illustrated by Bandel (1998) as *S. brevis* is, in fact, *S. levigata* (Iredale, 1908; see above).

Sinezona pacifica (Oliver, 1915)

(Figs 16–18)

Schismope pacificus Oliver, 1915: 514, pl. 9, figs 6, 6*a*.
Sinezona pacificus [sic]. Brook & Marshall, 1998: 214.
Daizona pacifica Bandel, 1998: 58, pl. 19, figs 6–8 (in part = *D. bandeli*, n. sp.). **New synonymy**.

Material examined

Neotype, Schismope pacificus Oliver. Here selected to facilitate recognition among other *Sinezona* species at Raoul Island; Raoul Island, Kermadec Islands, New Zealand (depth not recorded); AMS C.162250 (which is also the holotype of *Daizona pacifica* Bandel).

Other material examined. Raoul Island, Kermadec Islands, alive (shallow dredging, depth not recorded; 65, M.212572); SE of Smith Bluff, 29°18.90′S, 177°56.40′W, 82–100 m (4, M.226900); off W side of Meyer Island, 15 m (55, M.153992).

Distribution

Raoul Island, Kermadec Islands, and Norfolk Island, 0–100 m (depth for living specimens not recorded, but certainly as shallow as 15 m).

Remarks

Daizona pacifica Bandel, 1998 is both a synonym and a homonym of *Schismope pacificus* Oliver, 1915. Because type material of *Schismope pacificus* Oliver, 1915 is probably no longer extant (Freeman *et al.* 1997) and in order to obviate confusion with another superficially similar species that occurs at the type locality (e.g. M.226874) and with others from elsewhere in the south-west Pacific, the holotype of *D. pacifica* (Bandel 1998, pl. 19, figs 6–8) is here designated as a neotype of *S. pacificus*.

Bandel's (1998) record of *D. pacifica* from Rangaunu Bay, New Zealand, is based on specimens of a distinct species, which is described below.

Incidentally, *Sinezona* is feminine (*Schismope* masculine), so the specific epithet under *Sinezona* is *pacifica* rather than *pacificus*.

Sinezona bandeli n. sp.

(Figs 19–21, 25, 26)

Daizona pacifica Bandel, 1998: 58 (in part).
Sinezona sp. 5: Spencer *et al.* (in press).

Material examined

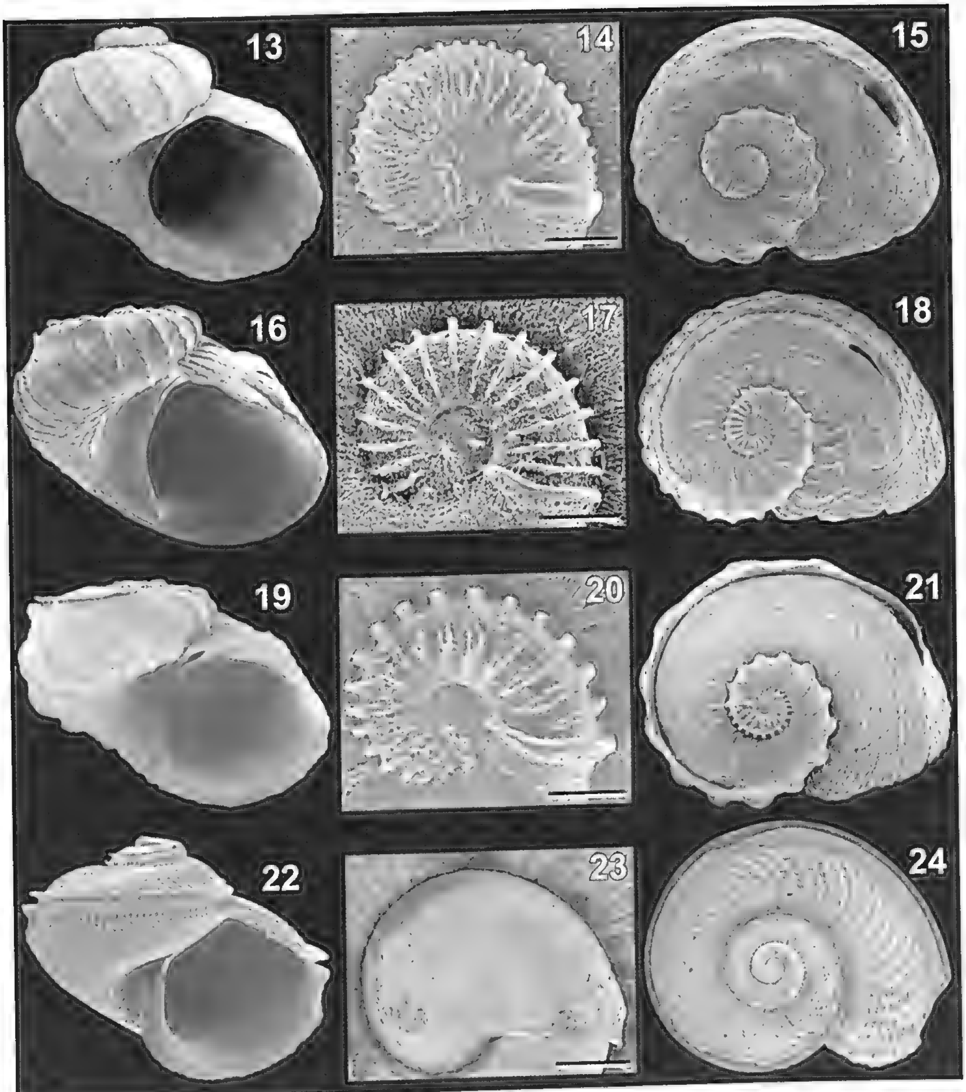
Holotype. Off Rangaunu Bay, New Zealand, 34°48.4′S, 173°19.5′E, alive, 25 m, 27 Jan. 1981, RV Tangaroa, NMNZ M.155919.

Paratypes. Same data as holotype (many, M.150283); off Rangaunu Bay, 34°49.6′S, 173°15.0′E, alive, 23 m (42, M.100505).

Other material examined. Off Three Kings Islands: Middlesex Bank, 33°57.0′S, 171°45.4′E, 98–103 m (3, M.150274); King Bank, 33°57.4′S, 172°19.4′E, 128–123 m (25, M.148572); Three Kings Trough, 34°00′S, 171°55′E, 805 m (11, M.150287); 34°01′S, 172°07′E, 622 m (16, M.150276); 13 km N of Great Island, 34°01.8′S, 172°12.0′E, 508 m (4, M.150288); 11 km NW of Great Island, 34°06.5′S, 172°04.7′E, 310 m (24, M.93865); off North-east Island, 34°08.5′S, 172°11′E, alive, 102 m (15, M.150282); reef between Great Island and Farmer Rocks, 34°09′S, 172°10′E, alive, 33 m (1, M.152626); North-west Bay, Great Island, 34°09.1′S, 172°08.4′E, alive, 23 m, airlifted from low mixed algae (mostly coralline) on boulders (4, M.137035); South-east Bay, Great Island, 34°09.5′S, 172°08.8′E, alive, 13–15 m, airlifted from under boulders (2, M.134905); 34°10′S, 172°12′E, 252 m (1, M.150273); off Princes Rocks, 34°10′S, 172°08′E, 14 m (5, M.150289); off South-west Island, 34°10′S, 172°08′E, 33 m (1, M.54040); Arch Pinnacle, Princes Rocks, 34°10.5′S, 172°03.0′E, 38 m (4, M.150334); Arch Pinnacle, Princes Islands, 34°10.5′S, 172°03.0′E, 44 m (2, M.150325); off N face of Hinemoa Island, 34°10.8′S, 172°02.6′E, 23 m (27, M.150277); 34°11′S, 172°10′E, 91 m (6, M.150281); off West Island, *Elingamite* wreck, 34°11′S, 172°03′E, 37 m (3, M.150317); 34°11.6′S, 172°10.9′E, 92 m (10, M.92071); S of Great Island, 34°14.1′S, 172°09.0′E, 192–202 m (6, M.150285); 39 km SW of Great Island, 34°17.6′S, 171°45.3′E, 427 m (1, M.94322). Off Spirits Bay, 34°22.58′S, 172°49.25′E, 49 m (3, M.152475); 34°23.55′S, 172°51.72′E, alive, 40 m (7, M.152479); 34°23.85′S, 172°47.55′E, alive, 32 m (28, M.152482); 34°23.87′S, 172°45.62′E, alive, 30 m (49, M.152483); 34°24.31′S, 172°49.95′E, 29 m (many, M.152485); 34°25.0′S, 172°46.6′E, 29 m (1, M.150275); 34°25.6′S, 172°48.2′E, 23 m (18, M.150280). N of Kerr Point, Tom Bowling Bay, 34°23.42′S, 172°59.18′E, 30 m (10, M.152477); Great Exhibition Bay, 34°33.4′S, 173°04.8′E, 63 m (1, M.150291); off Waikuku Beach, 47 m (5, M.150327); immediately outside Whangaroa Harbour entrance, 35°00.35′S, 173°45.7′E, alive, 25 m (1, M.152627); Whangaroa Harbour entrance, main channel, 35°02′S, 173°45′E, 20 m (5, M.150279). Bay of Islands: Waewaetorea Passage, 35°12.4′S, 174°13.3′E, 4 m (6, M.49405); 35°12.8′S, 174°15.6′E, 20–32 m (3, M.150315); Oke Bay, 35°13.4′S, 174°16.1′E, 3–5 m (1, M.150326); Paraoa Bay Point, 35°15.8′S, 174°10.4′E, 7 m (2, M.49467). Off Poor Knights Islands, 46 m (30, M.150329); off Poor Knights Islands (2, M.150333); Bartle's Bay, Aorangi Island, Poor Knights Islands, 35°28.5′S, 174°44.3′E, alive, stone washings, low tide (6, M.150323); between Marsden Point and Calliope Bank, Whangarei Harbour entrance, 35°50.2′S, 174°30.5′E, 20–25 m (1, M.150321); North Reef, of NW tip of Goat Island, Leigh, 36°16.2′S, 174°47.7′E, 18 m (2, M.150278); off E side of Ruamahua-nui Island, Aldermen Islands, 36°57.2′S, 176°05.8′E, 38 m (1, M.150292); off E side of Mayor Island, 37°18.9′S, 176°16.2E, 59–74 m (2, M.66513); Ranfurly Bank, East Cape, 37°33.4′S, 178°48.3′E, 106–103 m (1, M.150284); Rungapapa Knoll, WNW of White Island, 37°33.8′S, 176°59.0′E, 188–228 m (6, M.150290).

Description

Shell turbiniform, up to 1.30 mm wide, wider than high, thin; spire low, summit almost horizontal; translucent white. Protoconch 230 μm wide, all but inner one-quarter to one-third of exposed part of whorl section traversed by strong, high, flat-topped axial costae, costa nearest nucleus tangential to and longer than those following; terminal varix strong, rounded. Teleoconch of up to approximately 1.8 rather regularly expanding whorls; ramp weakly convex, almost horizontal on first whorl, thereafter gently sloping; side between selenizone and periphery shallowly concave; periphery and base smoothly continuous, rounded; umbilical rim angulate, wall steep and weakly convex. Selenizone strongly adapical, commencing shortly after start of last quarter of first whorl, rims closing



Figs 13–24. Shells of *Sinezona* and *Thieleella* species. *13–15*, *Sinezona brevis* (Hedley, 1904), Island Bay, Wellington, low tide, M.150342 (width 1.10 mm). *16–18*, *Sinezona pacifica* (Oliver, 1915), Raoul Island, Kermadec Islands, M.212572 (width 1.00 mm). *19–21*, *Sinezona bandeli* n. sp., off Rangaunu Bay, 25 m, paratype, M.150283 (*19*, width 1.20 mm); holotype, M.155919 (*20*, *21*, width 1.13 mm). *22–24*, *Thieleella flemingi* n. sp., Pegasus Canyon, off Banks Peninsula, 512–1006 m, M.52884 (width 2.02 mm). Scale bars: 50 μm.

together to form terminal foramen at shell diameter 0.9–1.00 mm or approximately one-sixth of whorl behind adult apertural rim, selenizone rims strongly elevated, internal septa weak. Sculptured throughout with crisp spiral threads and commarginal axial riblets. Spirals of similar size throughout, commencing shortly after appearance of selenizone, multiplying by intercalation. Axials stronger than spirals throughout, commencing immediately, approximately 14 on first whorl, strong and entirely traversing first 0.75 whorl; following appearance of selenizone weaker and restricted to inner part of ramp, evanescent at approximately middle of ramp, progressively weakening with increasing shell

size; below selenizone absent from concave side, strong and progressively enlarging on periphery and base, evanescent at umbilical rim, 9–12 last whorl in adults, becoming obsolete on last quarter whorl. Entire surface with crisp microsculpture of granules and commarginal growth lines. Aperture subcircular, peristome discontinuous, parietal area narrow, inducture of moderate thickness. Radula (Figs 25, 26) $n + 4 + 1 + 4 + n$. Central tooth broad, broad cutting area with seven similar cusps; lateral teeth with broad, outwardly bowed bases and narrow cutting areas, cutting areas of inner three pairs with two or three similar cusps, outermost pair with single cusp. Marginal teeth numerous, innermost pair massive, shaft flanged to interlock with adjacent teeth, cutting area tapered; outer marginals slender, each with five or more sharp slender cusps.

Distribution

Three Kings Islands and north-eastern North Island as far south as East Cape, New Zealand, 0–805 m; taken alive at extreme low tide (stone washings, Poor Knights Islands) to 102 m from clean bryozoan/shell and shell substrata, locally common.

Remarks

Specimens from off Rangaunu Bay (M.15005) were misidentified by Bandel (1998) as *Daizona pacifica* Bandel, 1998, which is both a synonym and a homonym of *Sinezona pacifica* (Oliver, 1915) from the same locality (Raoul Island, Kermadec Islands). Compared with *S. pacifica*, *S. bandeli* differs in a number of details, including larger and more strongly ribbed protoconch (width 230 *v.* 200 µm), stronger and fewer axial costae on the teleoconch, more steeply tapered sides and later closure of the selenizone to form a foramen (shell diameter 0.90–1.00 *v.* 0.70–0.80 mm). *Sinezona bandeli* bears a more superficial resemblance to *S. laqueus* (Finlay, 1926), with which it is sympatric, but differs in numerous details, including a smaller protoconch, smaller maximum size, smaller size relative to the number of whorls, much weaker septa within the selenizone, more shallowly concave sides, weaker axial costae and shorter selenizone.

Etymology

After Klaus Bandel, University of Hamburg.

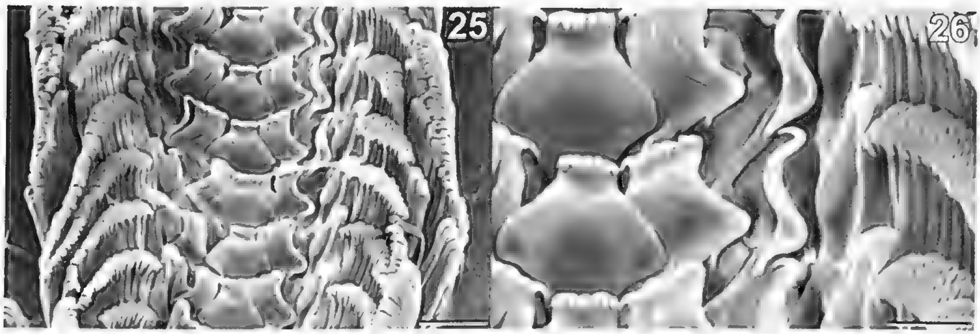
Subfamily **ANATOMINAE** McLean, 1989

Genus ***Thieleella*** Bandel, 1998

Thieleella Bandel, 1998: 35. Type species (by original designation): *Scissurella amoena* Thiele, 1912; Recent, Antarctica.

Remarks

Thieleella was introduced for species closely similar to species of *Anatoma* in teleoconch morphology but with a protoconch sculptured with a network of threads that enclose irregular polygonal spaces, rather than fine granules that are typically grouped into more or less distinct wavy axial lines. The protoconch of the type species of *Hainella* Bandel, 1998 (*Scissurella euglypta* Pelseneer, 1903; Recent, Antarctica) is similar to that in *Anatoma* species, as is the teleoconch, and it is difficult to see how *Hainella* could be separated from *Anatoma* on the basis of shell morphology.



Figs 25, 26. Radula. *Sinezona bandeli* n. sp., off Rangaunu Bay, 25 m, paratype, M.150283. Scale bars: *25*, 100 µm; *26*, 50 µm.

Thieleella protoconch sculpture is strikingly similar to that of the New Zealand species *Schismope lyallensis* Finlay, 1926, which was referred to *Sukashitrochus* Habe & Kosuge, 1964 on the basis of similarity to its type species (*Scissurella carinata* A. Adams, 1862) in teleoconch morphology (Marshall 1993). Other species referred to *Sukashitrochus* by Bandel (1998) on the basis of teleoconch morphology have several types of protoconch sculpture, the significance of which remains to be established (protoconch of *S. carinata* unknown).

Thieleella flemingi n. sp.

(Figs 22–24)

Schizotrochus mantelli. – Fleming, 1948: 84, pl. 8, fig. 3 (not *Scissurella mantelli* Woodward, 1859); Fleming, 1951: 136 (not Woodward).
Anatoma mantelli. – Powell, 1979: 36, pl. 14, fig. 1 (not Woodward).

Material examined

Holotype. The 'neotype' of *S. mantelli sensu* Fleming (1948) not Woodward, 1859; Daggs Sound, inside a rock bar (i.e. moraine), Fiordland, New Zealand, 106 m; NZGS TM426.

Other material examined. S of Kaikoura Peninsula, 42°35′S, 173°41′E, alive, 640 m (1, M.53684); Conway Rise, off Kaikoura, alive, 400 m (2, M.150211); wall of Pegasus Canyon, NE of Banks Peninsula, 43°14′S, 173°39′E, alive, 512–1006 m (2, M.52884). Thompson Basin floor Thompson Sound, 45°13.00′S, 166°57.96′E, 350 m, two stations (2, M.138880; 5, M.138535); 45°13.06′S, 166°58.01′E, 350 m, two stations (13, M.138780; 5, M.138837); 45°14.36′S, 166°58.96′E, 319–324 m (1, M.150711); 45°14.38′S, 166°58.87′E, 340–362 m (18, M.150524). Bradshaw Basin floor, Bradshaw Sound, 45°17.25′S, 167°02.46′E, 417 m (2, M.150652); 45°17.3′S, 167°02.6′E, 415 m (10, M.138409). Doubtful Sound, Utah Basin floor, 45°17.9′S, 166°55.5′E, 400 m (3, M.138624); Kellard Basin floor, 45°21.30′S, 167°03.36′E, 376 m (1, M.138598); Crooked Arm entrance sill (i.e. moraine), 45°21.41′S, 167°01.79′E, 54–60 m (4, M.138985). Long Sound narrows, Preservation Inlet, 35–40 m (probably moraine; 1, NZGS RM2212); head of Karitane Canyon, NE of Taiaroa Head, 45°38.5′S, 171°05.0′E, 585–530 m (3, M.51230); off East Otago, 45°45′S, 171°02′E, 520–600 m (1, M.150337); off Antipodes Islands, 49°40′S, 178°53′E, alive, 450–476 m (1, M.131196).

Description

Shell turbiniform, up to 3.70 mm wide, wider than high, thin, spire 0.43–0.85× height of aperture, translucent white. Protoconch 200 µm wide, sculptured with irregular network of fine, crisp threads; strong, rounded, subterminal varix. Teleoconch of up to 3.4 rather

regularly expanding whorls, ramp broadly and evenly rounded, abapical selenizone rim peripheral; base broadly rounded, evenly curving into narrow, deep umbilicus. Selenizone strongly abapical, commencing at end of first 0.75 whorl, terminating at aperture as open slit, rims strongly elevated; distance between selenizone and succeeding whorl approximately width of selenizone or less on first three whorls, thereafter widening to varying degrees due to descent of last adult whorl. Sculptured throughout with crisp, reticulating spiral threads and commarginal axial riblets, spirals of similar size throughout; axials stronger than spirals on ramp and as strong as spirals on side and base, approximately twice as many on adapical side of selenizone rim, in selenizone and on base and side than on spire. Spiral threads multiplying by intercalation, one commencing immediately and extending to start of selenizone, others commencing at end of first whorl, approximately nine on ramp at end of second whorl, up to 20 on ramp and 40 on base on last whorl of large specimens. Aperture subcircular, peristome discontinuous, parietal area broad, inducture extremely thin, rim of strongly flared abapical part of inner lip intersecting prominent angulation that extends up umbilical wall.

Distribution

Off South Island east coast and Antipodes Islands, New Zealand, living at 400–1006 m (with certainty as deep as 640 m), and Fiordland, 319–417 m (shells only). Shells from the Crooked Arm entrance sill (54–60 m) are from a moraine deposit, occurring together with common shells of other bathyal molluscs and corals that undoubtedly originated from the floor of the deep glaciated basin behind the sill. The holotype (106 m) and the shell from Long Sound narrows (35–40 m) are almost certainly also from moraines.

Remarks

Woodward (1859) introduced *Scissurella mantelli* for a shell reputedly obtained from a sample of 'menaccanite' sand obtained 'in New Zealand' by Walter Mantell. Interpretation of this species has been based consistently on the illustration indicated as representing *S. mantelli* that accompanied the original description (Woodward 1859, pl. 46, fig. 8). On this basis, Fleming (1948) identified similar New Zealand specimens as *S. mantelli* and, subsequently (Fleming 1951), selected one of them as the neotype.

When introducing *S. mantelli*, Woodward (1859: figs 1–7) illustrated three scissurellid species: '*Scissurella elegans* d'Orbigny, 1824' (misidentified; see above), *S. crispata* Fleming, 1828 (fig. '9'), and *S. mantelli* (fig. '8'). Woodward (1859) described *S. mantelli* by contrasting it with *S. elegans* alone, stating that it was '... larger, more depressed, more strongly ornamented, and has a longer scissural band'. From his illustrations, there can be no doubt that the description is actually based on the specimen depicted at his fig. 9 and that the names *S. mantelli* and *S. crispata* are simply transposed in the legend, so the putative New Zealand species is really the one depicted at fig. 9. No species known from the New Zealand region (named or un-named) matches the original illustration, suggesting that Woodward's specimen was mislocalised. Accordingly, Fleming's (1951) neotype of *S.* '*mantelli*' (not Woodward) represents an unnamed species (of *Thieleella*), for which a substitute name is provided here.

The provenance of Mantell's specimen has long been a mystery to New Zealand workers because the sample of 'menaccanite' sand (i.e. ironsand) from which it reputedly came was almost certainly from a North Island west coast beach (Dawson 1991) and because ironsand

does not occur where *S.* '*mantelli*' = *T. flemingi* has been found, specifically (and uncommonly) off the southern South Island and the Antipodes Islands at 319–1006 m depth (depth records from moraines excluded). Further evidence that the sample was mislocalised is Woodward's (1859) statement that it included a species of *Ringicula* Deshayes, 1838, no member of that genus having been recorded from depths shallower than 165 m off mainland New Zealand, yet faunas from this deep in the area were not sampled until later in the 19th century (*Challenger* Expedition). While it seems impossible to know for sure, it seems likely to me that the original specimen of *S. mantelli* Woodward is actually a subadult of a species of *Reussella* Bandel, 1998, perhaps *R. plicata* (Hedley, 1899) or a similar species, which are not uncommon in sediments from shallow tropical lagoons in the Western Pacific where, indeed, they may occur together with *Ringicula* species. In the absence of type material, or even a type locality, *S. mantelli* Woodward should be dismissed as a *nomen dubium*.

Etymology

After the late Sir Charles Fleming, who fostered my early interest in malacology.

Subfamily **LAROCHEINAE** Finlay, 1927

Genus ***Trogloconcha*** Kase & Kano, 2002

Trogloconcha Kase & Kano, 2002: 26. Type species (by original designation): *Trogloconcha ohashii* Kase & Kano, 2002; Recent, tropical and subtropical Indo-Pacific.

Trogloconcha* sp. cf. *tesselata Kase & Kano, 2002

Larochea miranda. Bandel, 1998: 66, pl. 23, figs 4, 5. Not Finlay, 1927.
Trogloconcha ohashii. Kase & Kano, 2002: 26 (in part).

Distribution

Swain Reef, Queensland.

Remarks

The Australian species identified as *Larochea miranda* by Bandel (1998) differs markedly from the New Zealand endemic species *L. miranda* in having a more central apex, more tightly coiled whorls and much stronger reticulate sculpture. This specimen was identified as *Trogloconcha ohashii* Kase & Kano, 2002, by Kase and Kano (2002), although from the illustrations it seems more likely to be *T. tesselata* Kase & Kano, 2002.

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Prochaetodermatidae of the Indian Ocean collected during Soviet VITYAZ cruises 1959–1964 (Mollusca : Aplacophora)

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Abstract

Four new aplacophoran mollusc species of Prochaetodermatidae (*Prochaetoderma arabicum* n. sp., *Chevroderma lusae* n. sp., *Chev. javanicum* n. sp., and *Chev. vityazi* n. sp.) and three new records (*Chev. turnerae* Scheltema, *Chev. paradoxum* Ivanov & Scheltema, *Claviderma laticarinatum* Ivanov & Scheltema) are added here to those described earlier for the western Indian Ocean and Arabian Sea and Atlantic Ocean. One of the species, the abyssal *Chev. turnerae*, is cosmopolitan throughout the Atlantic Ocean and is here reported from the eastern and western Indian Ocean. *Prochaetoderma arabicum* n. sp. is the only species in the genus *Prochaetoderma* that has been collected in the Indian Ocean/Arabian Sea. Two eastern Indian Ocean species, both with a curiously long narrow posterium, are superficially similar; one, *Chev. javanicum*, occurs at hadal depths in the Java Trench and the other, *Chev. vityazi*, was collected from the lower continental slope. So far, no prochaetodermatid species has been collected from the Indian Ocean at depths less than 1000 m.

Additional keywords: biogeography, deep sea, depth distribution, radula, spicules.

Introduction

Aplacophoran molluscs are a common, and sometimes abundant, part of the shelf, bathyal, abyssal and hadal oceanic benthic macrofauna from depths of <200 to >9000 m. Although they occur in most dredge and quantitative samples taken at these depths, they remain relatively unknown. General accounts of the two taxa comprising the Aplacophora, the Neomeniomorpha or Solenogastres and Chaetodermomorpha or Caudofoveata may be found in Salvini-Plawen (1985), Scheltema (1998) and Scheltema *et al.* (1994).

The Prochaetodermatidae is a family of mostly deep-sea Chaetodermomorpha that is distributed globally. It is comprised so far of five genera and 25 species. Their importance to the deep-sea benthos is belied by the low number of species because, in many localities, they are a dominant part of the benthos in numerical abundance (Grassle and Maciolek 1992; Scheltema 1997). They are small animals, usually <5 mm, and are covered with glistening aragonite spicules (C. C. Wu in Acknowledgments of Scheltema 1985) that identify them as belonging to the Aplacophora. So far, species of Prochaetodermatidae have been described from the north-west, south-west, north central, and north-east to south-east Atlantic, the Mediterranean Sea, the north, north central and north-west Pacific, the Indian Ocean and off south-eastern Australia at depths ranging between 100 and >9000 m (Kowalevsky 1901; Schwabl 1963; Salvini-Plawen 1972, 1992, 1999; Scheltema 1985, 1989; Belyaev 1989; Ivanov 1995, 1996; Scheltema and Ivanov 2000, 2001; Ivanov and Scheltema 2001*a*, 2001*b*). Some species and all genera have broad geographic ranges (Scheltema 1985; Scheltema and Ivanov 2000, 2001; Ivanov and Scheltema 2001*a*, 2001*b*).

The descriptions of prochaetodermatid species are continued here for Soviet collections made in the Indian Ocean from 1959 to 1964, adding further species to those already

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described from the western Indian Ocean and Arabian Sea (Ivanov and Scheltema 2001*a*). It is our plan eventually to study existing collections from all oceans. We expect that hypotheses about the biogeography of the deep-sea fauna will finally result from the distributions of prochaetodermatid species as they become known.

Materials and methods

Fifty prochaetodermatid specimens collected in the Indian Ocean and Java Trench during cruises of the Soviet research vessel VITYAZ from 1959 to 1964 were examined (Table 1). These specimens are in addition to the 12 VITYAZ specimens reported earlier by Ivanov and Scheltema (2001*a*; see Table 1). Methods for studying prochaetodermatids and the taxonomic characters used here are given in full in Scheltema and Ivanov (2000) and Ivanov and Scheltema (2001*a*). The characters are based on external appearance, including measurements of the anterium, trunk, shank and knob, and the ratio of posterium length (shank + knob) to trunk length (Fig. 58), on the morphology of spicules from anterior to posterior, including the base, blade, longitudinal axis and isochromes (lines of equal colour when viewed under crossed polarised light indicated by dotted lines; e.g. Fig. 6) and on the morphology of isolated radulae and jaws. Greatest dimensions are given for all measurements. In cases in which descriptions of new species rely only on the holotype, or on the holotype and a single or few paratypes, radula dissections were not made.

All material is deposited in the Zoological Museum of the University of Moscow (ZMUM).

Table 1. Prochaetodermatidae material examined from VITYAZ cruises in the eastern and western Indian Ocean 1959–1964 (see also Ivanov and Scheltema 2001*a*: table 1)

Stn	Gear	Depth[A] m	Date d.m.y	Latitude	Longitude	Species[B] *jav*	*vit*	*lus*	*par*	*tur*	*ar*	*lat*	*ga*
4530	TR[C]	6935	01.11.59	10°17'S	110°20'E	22							
4535	TR	6820	04.11.59	10°08'S	107°55'E	15							
4666	GR[C]	3888	05.03.60	06°53'S	53°36'E					1			
4697[D]	GR	4144	22.03.60	03°48'S	53°00'E				1				
4699	GR	3272	25.03.60	03°30'S	55°46'E					1			
4725[D]	GR	3070	15.04.60	13°36'N	54°28'E								1
4795[D]	GR	2833	29.10.60	11°07'N	52°13'E								2
4799[D]	GR	4458	01.11.60	08°21'N	56°17'E				1				
4800[D]	GR	3470	01.11.60	09°33'N	57°02'E				1				
4804[D]	GR	3717	04.11.60	17°18'N	58°58'E								4
4806	GR	1730	05.11.60	21°09'N	59°39'E						2		
4852	GR	3840	25.11.60	15°07'N	65°57'E			1		1			
4854	GR	3160	26.11.60	19°13'N	65°56'E			1					
4858	GR	3530	28.11.60	23°12'N	64°12'E					1?			
4933[D]	GR	2030	31.01.61	18°57'N	87°00'E							3[E]	
4939	GR	3620	04.02.61	08°54'N	87°02'E			1					
4963	GR	2520	01.03.61	16°09'N	92°37'E					1			
5292	GR	3850	30.10.62	05°05N	91°45'E				1				
5307	GR	2875	29.10.64	14°51.7'N	88°09.9'E		1						
Totals						37	1	3	4	5	2	3	7

[A]Minimum depth.
[B]*jav*, *Chevroderma javanicum*; *vit*, *Chevroderma vityazi*; *lus*, *Chevroderma lusae*; *par*, *Chevroderma paradoxum*; *tur*, *Chevroderma turnerae*; *ar*, *Prochaetoderma arabicum*; *lat*, *Claviderma laticarinatum*; *ga*, *Claviderma gagei*.
[C]TR, trawl; GR, unspecified grab.
[D]Reported in Ivanov and Scheltema 2001*a*.
[E]Including one new record.

Key to genera of Indian Ocean/Arabian Sea Prochaetodermatidae based on trunk spicules and number of oral shield spicules

1. Medial groove and chevron-shaped growth lines and base (Figs 29–35, 48–56), two rows of oral shield spicules . . . . *Chevroderma*
   Without medial groove, growth lines straight or curved, one or more rows of oral shield spicules 2
2. Spicules adpressed. 3
   Blade of spicule bent outwards from body 4
3. Spicules flat, longitudinal axis straight (Figs 6–10, 15–19), two rows of oral shield spicules . . . . *Prochaetoderma*
   Base and blade of spicules curved towards body, longitudinal axis curved, ≥3 rows of oral shield spicules . . . . *Claviderma*
4. Plane of spicule base flat, spicule blade width one- to two-thirds base width, three rows of oral shield spicules . . . . *Spathoderma*
   Base of spicule transversely curved, very broad, blade narrow, one-fifth or less base width, one to two rows of oral shield spicules . . . . *Niteomica*

Taxonomy

Family **PROCHAETODERMATIDAE** Salvini-Plawen, 1972

Prochaetodermatidae Salvini-Plawen, 1969: 57 (without diagnosis).
Prochaetodermatidae Salvini-Plawen, 1972: 37.

Diagnosis

Aplacophorans with a divided oral shield (Fig. 2) and jaws (Figs 46, 47; *in situ* Fig. 65, arrowhead), with posterium usually narrow and tail-like (Figs 65–68).

Genus ***Prochaetoderma*** Thiele, 1902

Prochaetoderma Thiele, 1902: 275. Salvini-Plawen, 1972: 37; Ivanov, 1981: 25; Scheltema, 1985: 498; Salvini-Plawen, 1992: 323; Salvini-Plawen, 1999: 79; Scheltema & Ivanov, 2000: 327.
Type species: *Chaetoderma radulifera* Kowalevsky, 1901, by monotypy.

Diagnosis

Spicules adpressed, parallel on trunk and posterium to longitudinal body axis or only on posterium. Planes of spicule base and blade flat or blade slightly curved towards body; base and blade not obviously offset or at an angle to each other or rotated relative to each other; longitudinal axis straight, isochromes symmetrical or nearly so; waist shallow, sometimes indistinct. Blade with short or long medial keel, edges convex, blade width approximately same as base width at waist. Oral shield spicules in two rows.

Distribution

Northern and southern Atlantic, Mediterranean Sea, Arabian Sea, western Pacific, from shelf to bathyal depths (includes unpublished data).

Prochaetoderma arabicum n. sp.

(Figs 1–19, 65, 69)

Material examined

Holotype. North-western Arabian Sea, 21°09′N, 59°39′E, 1730 m, VITYAZ stn 4806, 5 Nov. 1960, ZMUM no. Le1-96.
Paratype. One individual, type locality, ZMUM no. Le1-97.

Diagnosis

Small, translucent, silky, broad trunk narrowing abruptly to narrow shank, posterium shorter than trunk (unnaturally stretched during processing in paratype); spicules symmetrical, short, thin, edges of base and blade convex, basally rounded, distally keeled with sharp point, base long, blade broad; fringing spicules longer than knob.

Description

Appearance (Figs 1–3, 11–14, 65). Small, translucent, silky sheen; trunk broad, indented approximately one-third distance from anterior; clear demarcation between trunk and shank; fringing spicules extending beyond knob; oral shield spicules not prominent.

Body measurements. Holotype: length 2.2 mm, anterium length 0.1 mm, trunk length 1.3 mm, greatest diameter posterior, 0.4 mm, shank length and width 0.5×0.1 mm, knob length 0.3 mm, length posterium/trunk 0.62; oral shield 0.1×1.5 mm.

Spicules (Figs 4–10,15–19). Most <100 µm long, thin, symmetrical, edges of both base and blade convex, proximally rounded, blade broad with sharp distal keel and point, thickest at and below waist, longitudinal axis straight; spicules from beside oral shield broadly sinuous, 43 µm long, 18 µm wide, 3.5 µm thick; from anterium, many pyramidal, not sharply keeled, edges straight to convex, 40×18×1–3 µm, some with distinct waist and base narrower than blade; from anterior trunk, to 100 µm long, base 56 µm long, 45 µm wide, longer and broader than blade, 45×18 µm, 4 µm thick; from shank, narrower, shorter and thinner than trunk spicules, 74 µm long × 3.5 µm thick, base 22×14 µm, shorter than blade, 52×9 µm, with a few broad (~38 µm), thin (<3 µm), nearly pyramidal spicules; knob spicules to approximately 65 µm long, with tapered base; fringing spicules to 145×12 µm.

Radula. Not examined; jaws appearing narrow under transmitted light in undissected animals (Fig. 65, arrowhead).

Distribution (Fig. 69)

Lower slope, western Arabian Sea.

Remarks

We consider that the elongate and extremely narrow posterium of the paratype (Fig. 11) is not natural, but a result of stretching during collecting and sieving. This species is the only member of the genus *Prochaetoderma* so far found in the Indian Ocean/Arabian Sea. It is distinguished from the Mediterranean and Atlantic species *P. raduliferum*, *P. boucheti* and *P. yongei* by a narrower posterium, by spicules with broader blades with more convex sides and less distal taper and by narrow shank spicules and from *P. atlanticum*, in which spicules are curved.

Etymology

Named for type locality.

Genus *Chevroderma* Scheltema, 1985

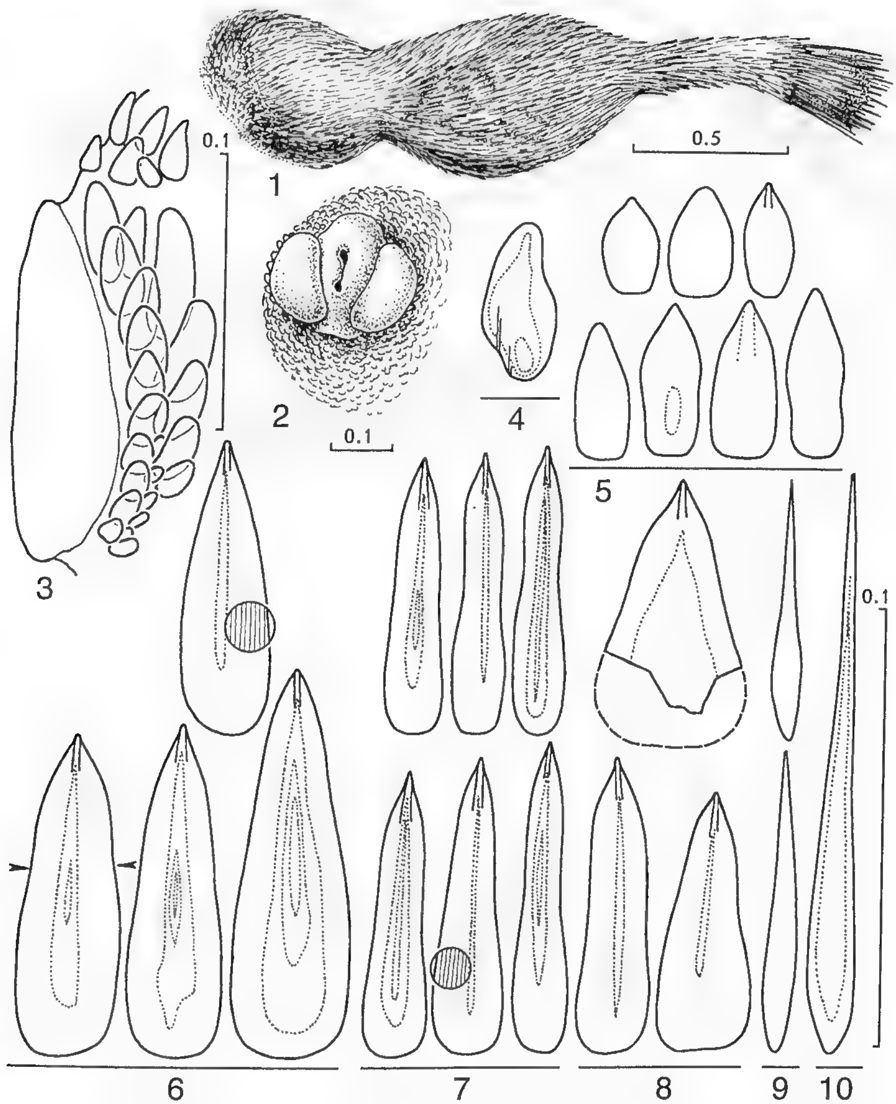
Chevroderma Scheltema, 1985: 512. Ivanov, 1996: 3; Scheltema & Ivanov, 2000: 344; Ivanov & Scheltema, 2001*a*: 14.

Prochaetoderma (*Chevroderma*) Salvini-Plawen, 1992: 323.

Type species: *Chevroderma turnerae* Scheltema, 1985: 512–516, by original designation.

Diagnosis

Spicules with usually distinct, but sometimes faint, medial groove that extends either entire length of spicule or only part way. Growth lines and base of spicules chevron-shaped. Plane

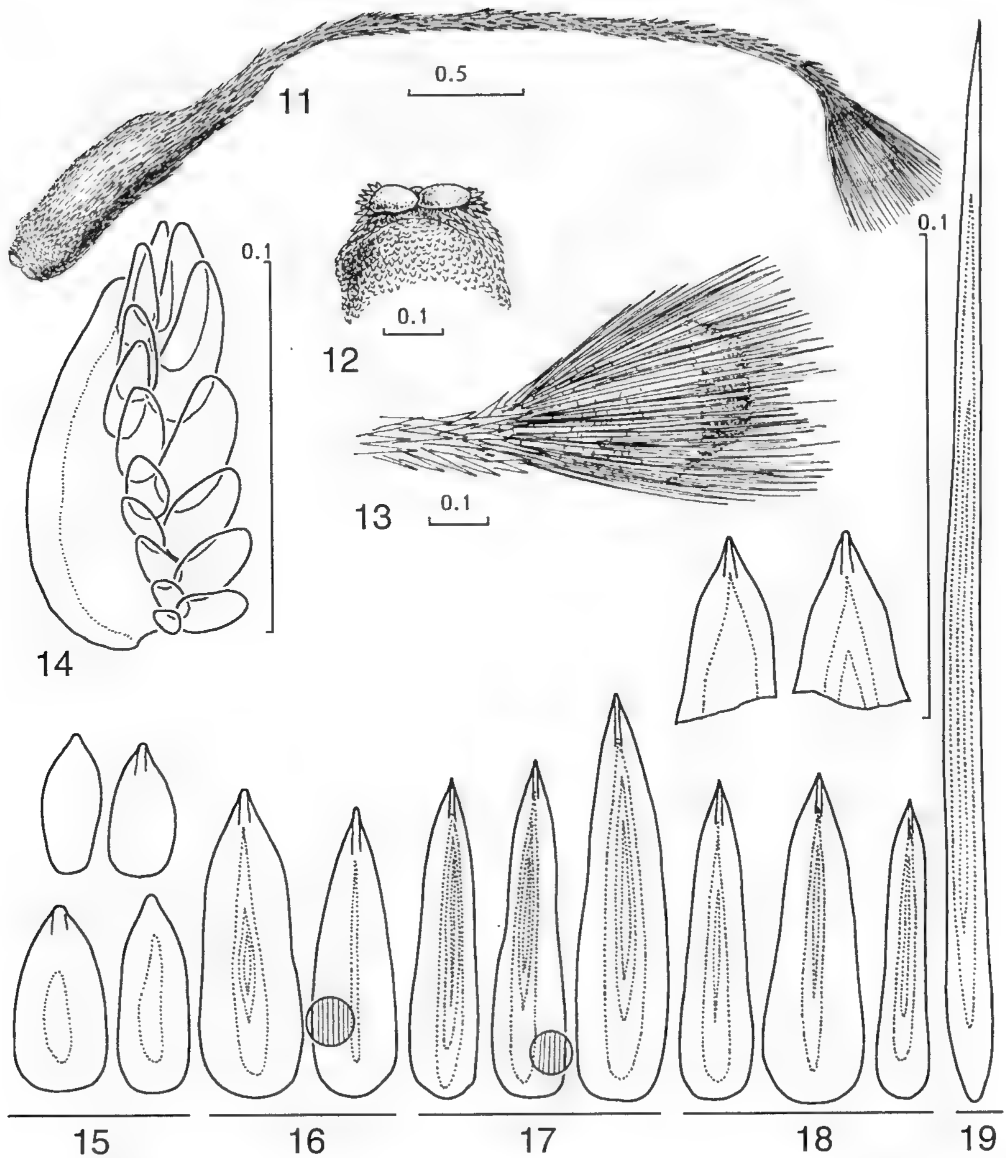


Figs 1–10. *Prochaetoderma arabicum* n. sp. holotype. *1*, entire; *2*, oral shield; *3*, oral shield spicules *in situ*; *4–10*, spicules of: *4*, oral shield; *5*, anterium; *6*, dorsal trunk (arrowheads indicate waist); *7*, anterior shank; *8*, posterior shank; *9*, knob; and *10*, fringe.

of spicule blade bent outwards from plane of base. Longitudinal axis straight to abruptly curved at waist. Waist usually distinct, blade narrower than base at waist, edges of blade nearly straight and tapered. Isochromes on each side of groove asymmetrical. Two rows of oral shield spicules.

Distribution

Species of *Chevroderma* have been found in most of the world's oceans: eastern and western north and south Atlantic, eastern and western Indian Ocean, eastern and western north and south Pacific and central north Pacific (Scheltema and Ivanov 2000, unpublished data). The shallowest depth recorded is 1427 m; the deepest, for *Chev. hadalis* Ivanov, is 8390 m in the



Figs 11–19. *Prochaetoderma arabicum* n. sp. paratype, posterium unnaturally stretched. *11*, entire; *12*, oral shield with barely discernible oral shield spicules; *13*, knob with long fringing spicules; *14*, oral shield spicules *in situ*; *15–19*, spicules of: *15*, anterium; *16*, trunk; *17*, anterior shank; *18*, posterior shank; and *19*, fringe.

Kurile-Kamchatka Trench and for an undescribed species also in the Pacific at >9000 m. All but one species, *Chev. scalpellum* Scheltema, are found at abyssal to hadal depths.

Chevroderma turnerae Scheltema, 1985

(Fig. 69)

Chevroderma turnerae Scheltema, 1985: 512–516. Scheltema and Ivanov, 2000: 345–348.

Material examined

Five individuals, one from each of five VITYAZ stations: 4666, 4699, 4852, 4858 (questionable identification) and 4963 (Table 1). ZMUM nos. Le1-106 through 110.

Diagnosis

Large, opaque, up to 5.5 mm in length and 0.8 mm in diameter, length posterium/trunk ranging from 0.32 to 1.36; oral shield large, oral shield spicules prominent; trunk spicules converging at prominent angle mid-dorsally, to 300 μm long, base long, blade short and bluntly pointed, thickest proximal to waist; radula and jaws large, teeth to 140 μm, jaws to 700 μm.

Distribution (Fig. 69)

Chevroderma turnerae was first described from the north-western Atlantic, the Argentine Basin, equatorial Atlantic and the entire eastern Atlantic. The five specimens recorded here extend the range into the western Indian Ocean and Bay of Bengal. Morphologically, they fall within the same range of differences that occur in Atlantic populations. The species is a lower slope and abyssal form.

Chevroderma lusae n. sp.

(Figs 20–35, 66, 69)

Material examined

Holotype. Bay of Bengal, 08°54′N, 87°02′E, 3620 m, VITYAZ stn 4939, 4 Feb. 1961, ZMUM no. Le1-98.

Paratype. One individual, eastern Arabian Sea, 15°07′N, 65°57′E, 3840 m, VITYAZ stn 4852, 25 Nov.1960, ZMUM no. Le1-99.

Other material examined. One individual, eastern Arabian Sea, 19°13′N, 65°56′E, 3160 m, VITYAZ stn 4854, 26 Nov. 1960, ZMUM no. Le1-100.

Diagnosis

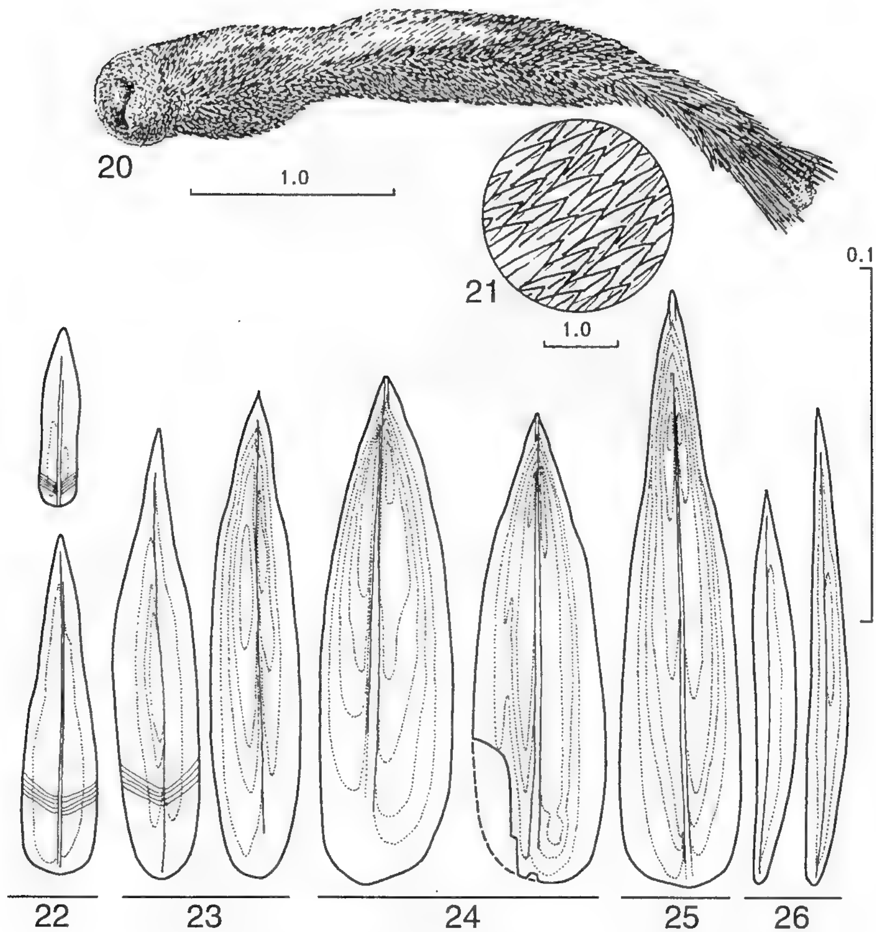
To nearly 4 mm, silky sheen, greatest diameter anterior, posterium one-third or less total length, trunk and shank spicules with indistinct or no waist, distally sharply pointed or nipple like, knob spicules tapered basally and distally.

Description

Appearance (Figs 20, 21, 27, 28, 66). Opaque to translucent, depending on degree of contraction, silky sheen; trunk indented between pharyngeal region and posterior part; posterium short, prominently set off from trunk; knob truncated, slanting; fringing spicules extending somewhat beyond knob; approximately nine oral shield spicules, not prominent.

Body measurements. Holotype largest individual, length 3.7 mm, anterium length 0.2 mm, trunk length and greatest width 2.4×0.5 mm, shank length and width 0.7×0.2 mm, knob 0.35 mm, length posterium/trunk 0.46; oral shield dimensions not determined.

Spicules (Figs 22–26, 29–35). Base broad with edges convexly curved, spicules on trunk and shank usually without waist, sharply pointed or nipple-like distally, thickest distally; spicules from beside oral shield symmetrical to curved, widest and thickest basally, to 63 μm long, 27 μm wide, 6 μm thick; from anterium, symmetrical or curved, thin, blade same width or broader than base, with medial groove, 47×13×1 μm; from ventral trunk, waist apparent, 94×34×4 μm, thickest on base, blade pyramidal on anterior ventral trunk, approximately one-third length of base; from ventral midtrunk, base longer and narrower; from dorsal midtrunk, 135–150×32×5 μm, thickened asymmetrically on either side of medial groove; from shank, like dorsal trunk spicules but thickened symmetrically on either



Figs 20–26. *Chevroderma lusae* n. sp. holotype. *20*, entire; *21*, enlargement of spicule coat; *22–26*, spicules from: *22*, anterium; *23*, midventral trunk; *24*, shank; *25*, posteriormost shank; and *26*, knob.

side of groove, 117×36×5 μm; from knob, straight or curved, with medial groove, tapered distally and basally, distally pointed, tapered and rounded basally, thickest medially, 144×14×5 μm; from fringe, thickest and widest basally, tapered basally, with medial groove, 232×17×6 μm.

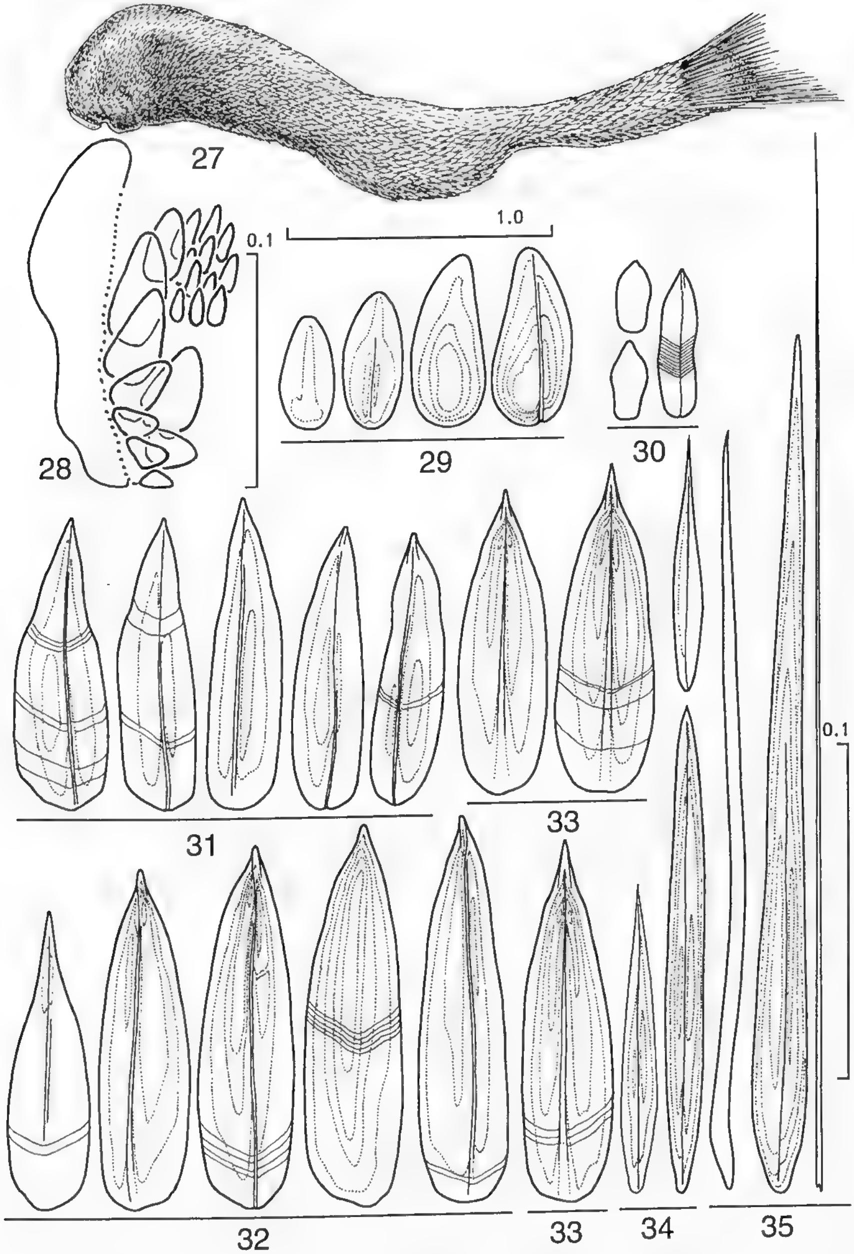
Radula. Not examined.

Distribution (Fig. 69)

Abyssal; Bay of Bengal and eastern Arabian Sea.

Remarks

The very short blade and indistinct waist of dorsal trunk spicules differentiates *Chevroderma lusae* from all but one described *Chevroderma* species, which have a long, tapered trunk blade and a distinct waist. In *Chev. javanicum* (below), the waist is also indistinct, but the trunk spicules are nearly twice the length and one-half to two-thirds the



Figs 27–35. *Chevroderma lusae* n. sp. paratype. *27*, entire; *28*, oral shield spicules *in situ*; *29–35*, spicules from: *29*, beside oral shield; *30*, anterium; *31*, anteroventral trunk; *32*, dorsal midtrunk; *33*, shank; *34*, knob; and *35*, fringe.

width. The individual from VITYAZ 4854, eastern Arabian Sea, is excluded from the type series because the sparseness of material makes it uncertain whether spicule differences (pronounced waist and longer blade of trunk spicules) indicate population or species differences.

Etymology

Named in honor of Valentina Lus, who gave careful attention to the Soviet Aplacophora collection when it was at the Shirshov Institute of Oceanology.

Chevroderma paradoxum Ivanov & Scheltema, 2001
(Fig. 69)

Chevroderma paradoxum Ivanov & Scheltema, 2001*a*: 14.

Material examined

One individual, Southern Bay of Bengal, 05°05′N, 91°45′E, 3850 m, VITYAZ stn 5292, 30 Oct. 1962, ZMUM no.Le1-101.

Diagnosis

Length <3 mm, greatest diameter anterior, 0.5 mm, compact, trunk tapering to shank usually without distinct demarcation, terminal end of knob truncated, slanted, oral shield small, height to 0.16 mm, oral shield spicules few, six in inner row, three in outer row.

Spicules. From anterium, symmetrical to asymmetrically curved; from trunk, with distinct waist, groove indistinct to slight, colour of isochromes on each side of groove indicating one side of spicule markedly thinner that the other, base longer than blade, thickest below waist, to 255 µm long; shank spicules similar to trunk spicules, to 325 µm long, base shorter than blade in more posterior spicules; knob spicules grooved, straight, tapered proximally and distally, to 176 µm long, or curved and bent proximally. Jaws to 424 µm long, 141 µm wide; radula teeth to 91 µm long, serrated membrane short with few, broad serrations.

Distribution (Fig. 69)

Abyssal, off Somalia and La Réunion and in the southern Bay of Bengal between 3240 and 4458 m.

Remarks

The compact body with usually no demarcation between trunk and shank distinguishes *Chev. paradoxum* from all other described species. The body shape in conjunction with the usually poorly defined groove on the spicules, small oral shield, few oral shield spicules and short radula tooth membrane with few serrations identify this species.

The distribution of *Chev. paradoxum* is herein extended to the eastern Indian Ocean. The spicules of the individual from this region are more distinctly grooved medially than of those previously described from the western Indian Ocean (Ivanov and Scheltema 2001*a*), but we regard the individuals as conspecific because the size and shape of the animals and the sizes and shapes of their spicules are the same, as are the number of oral shield spicules. We consider the distinctness of the groove in the Bay of Bengal individual, the only difference we could see, to be a population and not a species difference.

Chevroderma javanicum n. sp.

(Figs 36–57, 67, 69)

Material examined

Holotype. Java Trench, 10°17′S, 110°20′E, 6935–7060 m, VITYAZ stn 4530, 1 Nov. 1959, ZMUM no. Le1-102.

Paratypes. Twenty-one individuals, type locality, ZMUM no. Le1-103; 15 individuals, Java Trench, 10°08′S, 107°55′E, 6820–6850 m, VITYAZ stn 4535, 4 Nov. 1959, ZMUM no. Le1-104.

Diagnosis

Body long, narrow, appearance slick, dorsal midline well defined, ventral midline broad and flattened, anterior part of trunk narrower than more posterior part; spicules long and narrow, blade extremely short, waist ill-defined; radula tooth membrane scarcely serrated.

Description

Appearance (Figs 36–38, 40–42, 67). Elongate, slender, spicules closely adpressed, glistening; dorsal and ventral midlines distinctly defined dorsally by sharp angle where left and right lateral spicules meet, ventrally by broad, flattened region covered by small spicules; midlines continuing distinctly onto anterior shank; shank long, very narrow, varying widely in length from one-third to more than one-half body length; trunk narrower anteriorly than posteriorly, then tapering to shank; knob cone shaped, fringing spicules extending beyond knob; anterium protruded, sometimes bulbous; oral shield small, oral shield spicules not prominent;

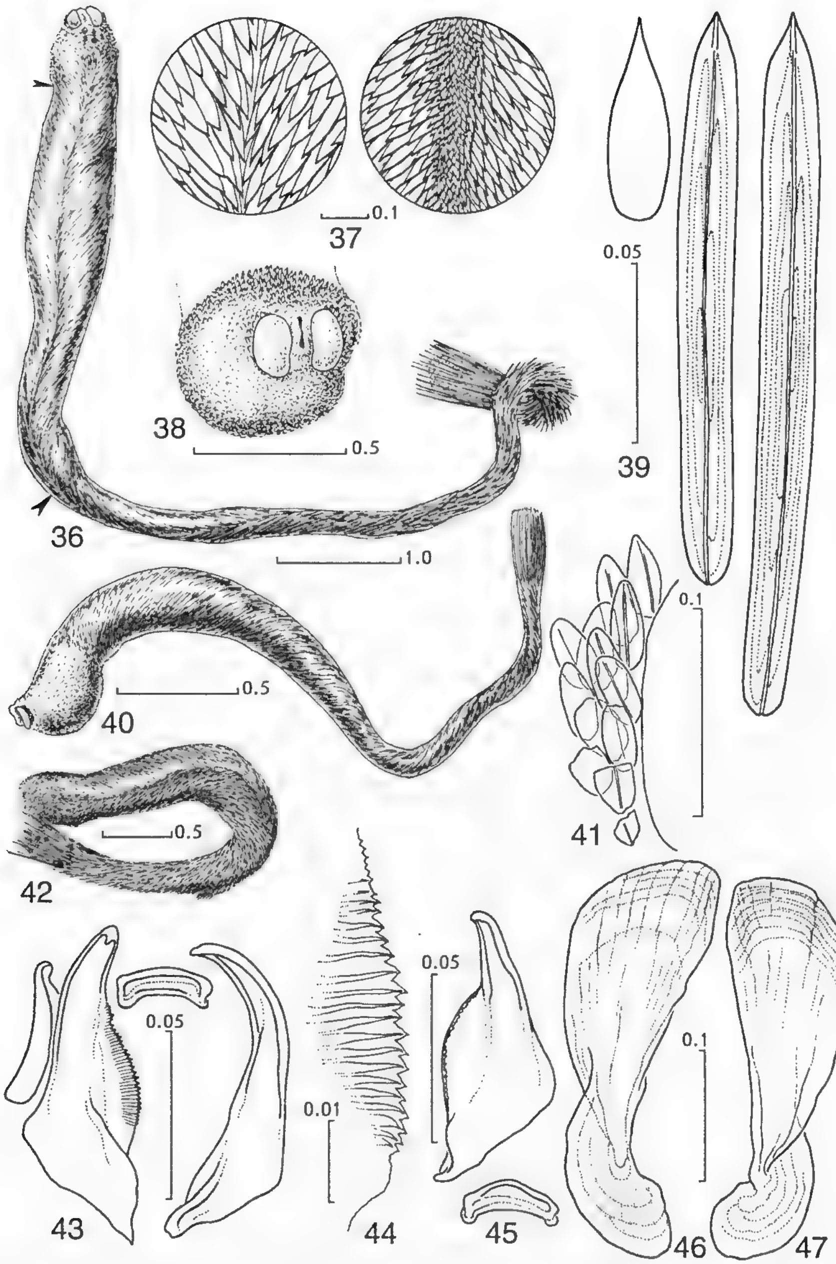
Body measurements. Holotype largest individual, length approximately 9.5 mm, anterium length 0.6 mm, trunk length 3.3 mm, diameter 0.5 mm anteriorly, 0.7 mm posteriorly, shank length and width approximately 5.0×0.2 mm, knob length 0.6 mm, length posterium/trunk approximately 2.0; oral shield height greatest dimension, 0.2 mm. Smallest individual 3.9 mm long, anterium 0.3 mm long, trunk 2.0×0.3 mm anteriorly, 0.5 mm posteriorly, shank 1.3×0.2 mm, knob 0.3 mm long, length posterium/trunk 1.0;

Spicules (Figs 39, 48–57). Removed for study only with difficulty; long, narrow, sides parallel, longitudinal axis straight to curved in frontal view, base curved towards body, thickest medially; waist indistinct, blade very short, 1/10 to 1/25 total spicule length; distally sharply pointed with a short keel and bent outwards from body; medial groove distinct, running length of spicule, chevron-shaped growth lines distinct only on anterior spicules, but many spicules basally chevron shaped; oral shield spicules subquadrate to pointed ovate, medially grooved, 45×22×4 μm; spicules just anterior to oral shield spicules ovate, 25×11×1 μm; from anterium to knob, major differences among most spicules in size, not shape, with trunk spicules diminishing in length from dorsal to ventral; anterium, 45×14×2 μm; anterior dorsal trunk, 260×22×7.5 μm; anterior ventral trunk, 130×17×6 μm; posterior dorsal trunk, 290×17×8 μm; posterior ventral trunk, 116×17×5 μm; shank, 270×14×9 μm; knob spicules tapered basally and distally with a sharp distal point, 226×17×8 μm; fringing spicules curved, 464×17×>10 μm.

Radula (Figs 43–47; two examined). Eight rows of teeth; jaws to 360 μm long, 87 μm wide in one specimen, but relatively broad, 128 μm, in the other; teeth to 100 μm; serrated membrane medial, 50 μm, scarcely serrated, some with ridges perpendicular to long axis of tooth; central plate short, deeply curved, 34×11 μm.

Distribution (Fig. 69)

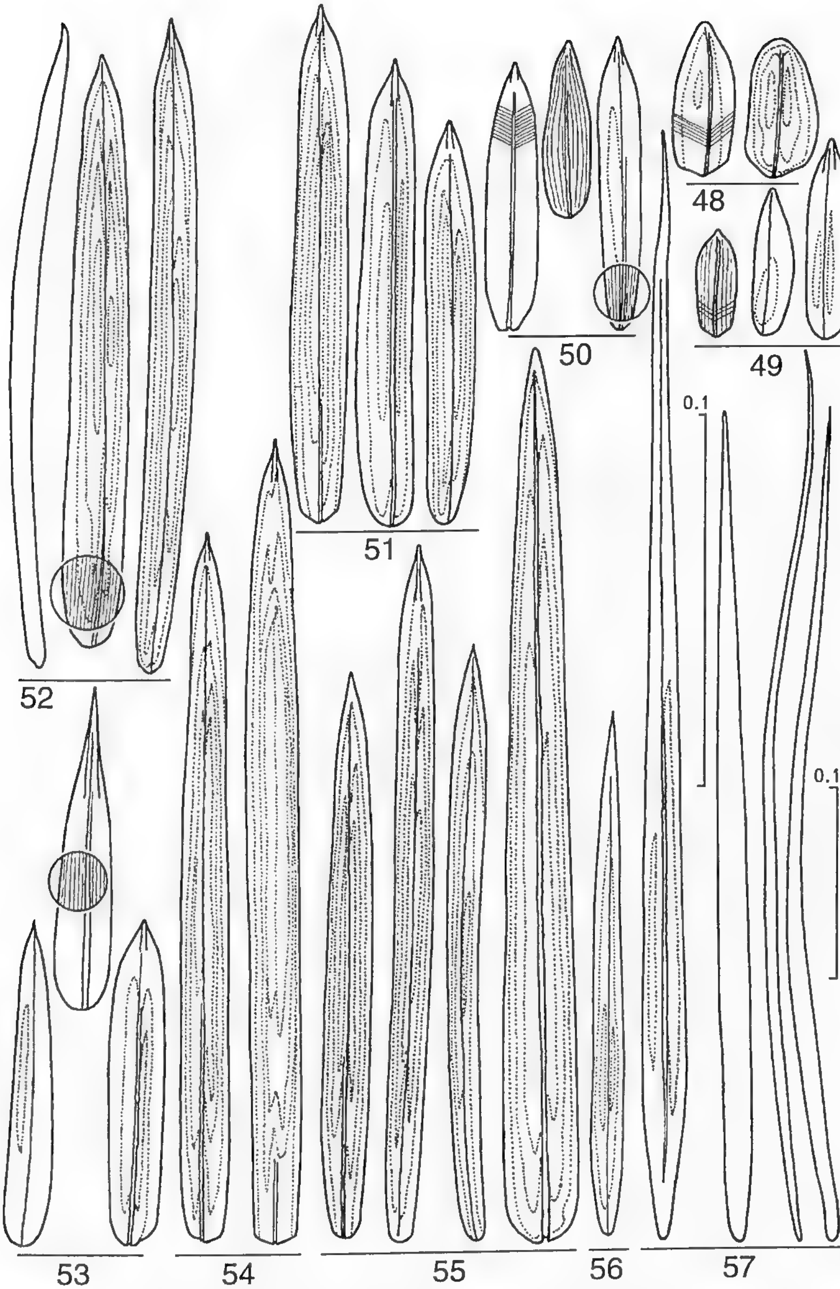
Hadal; Java Trench.



Figs 36–47. *Chevroderma javanicum* n. sp. *36–39*, holotype; *36*, entire, trunk delimited by arrowheads; *37*, dorsal (left) and ventral arrangement of midline spicules; *38*, oral shield; *39*, spicules from ventral midline (left) and lateral trunk; *40*, *41*, paratype, VITYAZ stn 4535, entire and oral shield spicules *in situ*; *42*, smallest individual, type locality, VITYAZ stn 4530; *43–47*, radula teeth, central plates and jaws of: *43*, *44*, *46*, an individual from type locality; *45*, *47*, paratype figured in *40*.

Remarks

The long, slender body and narrow spicules with a short blade of *Chevroderma javanicum* are distinguishing characters. *Chevroderma javanicum* is morphologically close to



Figs 48–57. *Chevroderma javanicum* n. sp. spicules from paratype (Fig. 40): *48*, beside oral shield; *49*, anterium; *50*, anterior ventral trunk; *51*, lateral anterior trunk; *52*, dorsal anterior trunk (note very short, outward bent blade of left spicule); *53*, posterior ventral trunk; *54*, dorsal posterior trunk; *55*, shank; *56*, knob; *57*, fringe.

Chev. vityazi, but can best be distinguished from it by the spicules, which, in *Chev. javanicum*, are longer, thicker and thickest medially and have an extremely short blade, giving the animals a smooth, glistening appearance.

Etymology

Named for the type locality.

Chevroderma vityazi n. sp.

(Figs 58–64, 68, 69)

Material examined

Holotype. Bay of Bengal, 14°51.7′N, 88°09.9′E, 2875 m, VITYAZ stn 5307, 29 Oct. 1964, ZMUM no. Le1-105.

Diagnosis

Somewhat shaggy, with narrow, long shank, oral shield spicules not prominent, trunk width probably even throughout, shank twice as wide near trunk as further posteriorly, knob cone-shaped.

Description

Appearance (Figs 58, 59, 68). Holotype only individual; spicule coat somewhat shaggy owing to outwardly bent spicule blades (Fig. 61, right spicule), spicules converging mid-dorsally and diverging midventrally; posterium narrow, long; trunk width probably same throughout length, although slightly broken specimen appears widest posteriorly; shank somewhat wider near trunk; posterium nearly twice trunk length; knob cone-shaped, fringing spicules extending beyond knob; oral shield small, higher than wide, oral shield spicules not prominent.

Body measurements. Holotype total length 3.5 mm, anterium approximately 0.2 mm, trunk 1.2 mm long, 0.3 mm in diameter, shank 1.8×0.1 mm, knob length 0.3 mm, length posterium/trunk 1.7; oral shield not measured.

Spicules (Figs 60–64). Long, narrow, widest at midpoint or just below midpoint, base tapered proximally, blade short, sharply tapered to point, waist distinct, thickest on base just below waist; spicules from between anterium and trunk to 74×16×1–2 μm thick; trunk spicules to 170×22×4 μm, blade to 34 μm long; shank spicules shorter and thinner than trunk spicules, to 150×20×4 μm and with slightly longer blade, to 38 μm; knob spicules tapered proximally and distally, relatively broad medially, to 117×9×3.5 μm, waist usually distinct, blade long, to 52 μm; fringe spicules with broad, short base, to 273×13×6 μm, blade length to 157 μm.

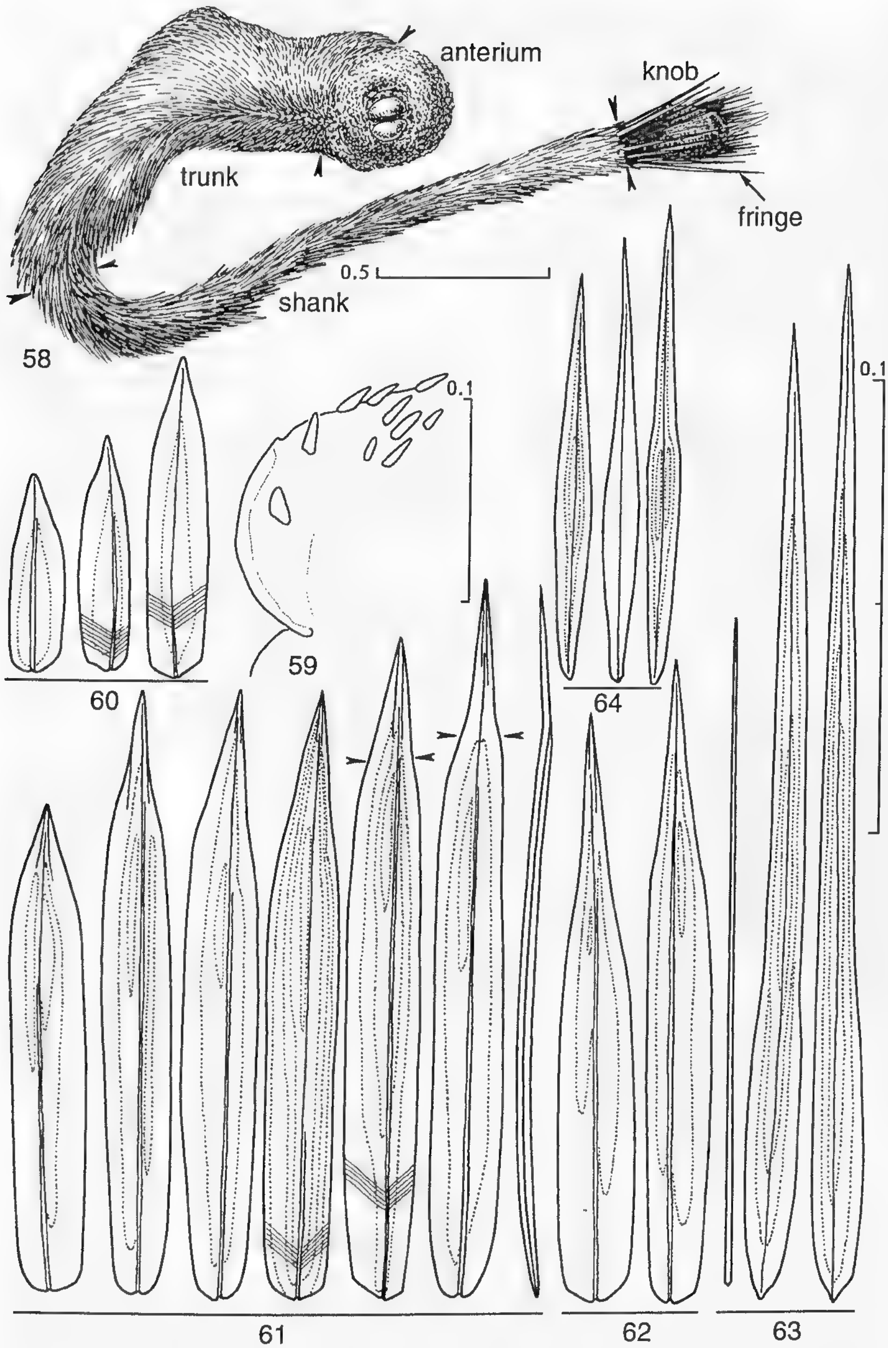
Radula. Not examined.

Distribution (Fig. 69)

Lower slope; Bay of Bengal.

Remarks

Chevroderma vityazi is similar to *Chev. javanicum*, but shorter spicules with a distinct waist, a slightly rough spicule coat and ventral midline that is not broad distinguish *Chev. vityazi* from *Chev. javanicum*.



Figs 58–64. *Chevroderma vityazi* n. sp. holotype. *58*, entire, with body regions indicated; *59*, a few spicules remaining *in situ* beside the oral shield; *60–64*, spicules from: *60*, between anterium and anterior trunk; *61*, mid-dorsal and lateral trunk (arrowheads indicate waist); *62*, shank; *63*, fringe; and *64*, knob.

Etymology

Named for the research vessel VITYAZ.

Genus *Claviderma* Scheltema & Ivanov, 2000

Rhabdoderma Scheltema, 1989: 56.
Claviderma Scheltema & Ivanov, 2000: 351. Ivanov & Scheltema, 2001*a*: 18.
Type species: *Rhabdoderma australe* Scheltema, 1989: 56 (original designation).

Diagnosis

Plane of spicule base and blade form single curve toward body, spicules closely adpressed, without keel. Longitudinal axis of spicules straight to slightly curved, waist distinct to indistinct, blade nearly as broad as base at waist, lateral edges slightly to markedly convex. Isochromes mostly symmetrical. Oral shield spicules in three or more rows.

Distribution

Known from western Atlantic south of 35°N to the Argentine Basin, eastern Atlantic from the Bay of Biscay to Cape Basin, Indian Ocean and south-western Pacific at depths between 1000 and 3800 m, except one species at depths between 93 and 143 m in the Bay of Biscay (Salvini-Plawen 1999; Scheltema and Ivanov 2000, 2001).

Claviderma laticarinatum Ivanov & Scheltema, 2001

(Fig. 69)

Claviderma laticarinatum Ivanov & Scheltema, 2001: 18.

Material examined

One individual, northern Bay of Bengal, 18°57′N, 87°00′E, 2030 m, VITYAZ stn 4933, 31 Jan. 1961. ZMUM no. Le1-111.

Diagnosis

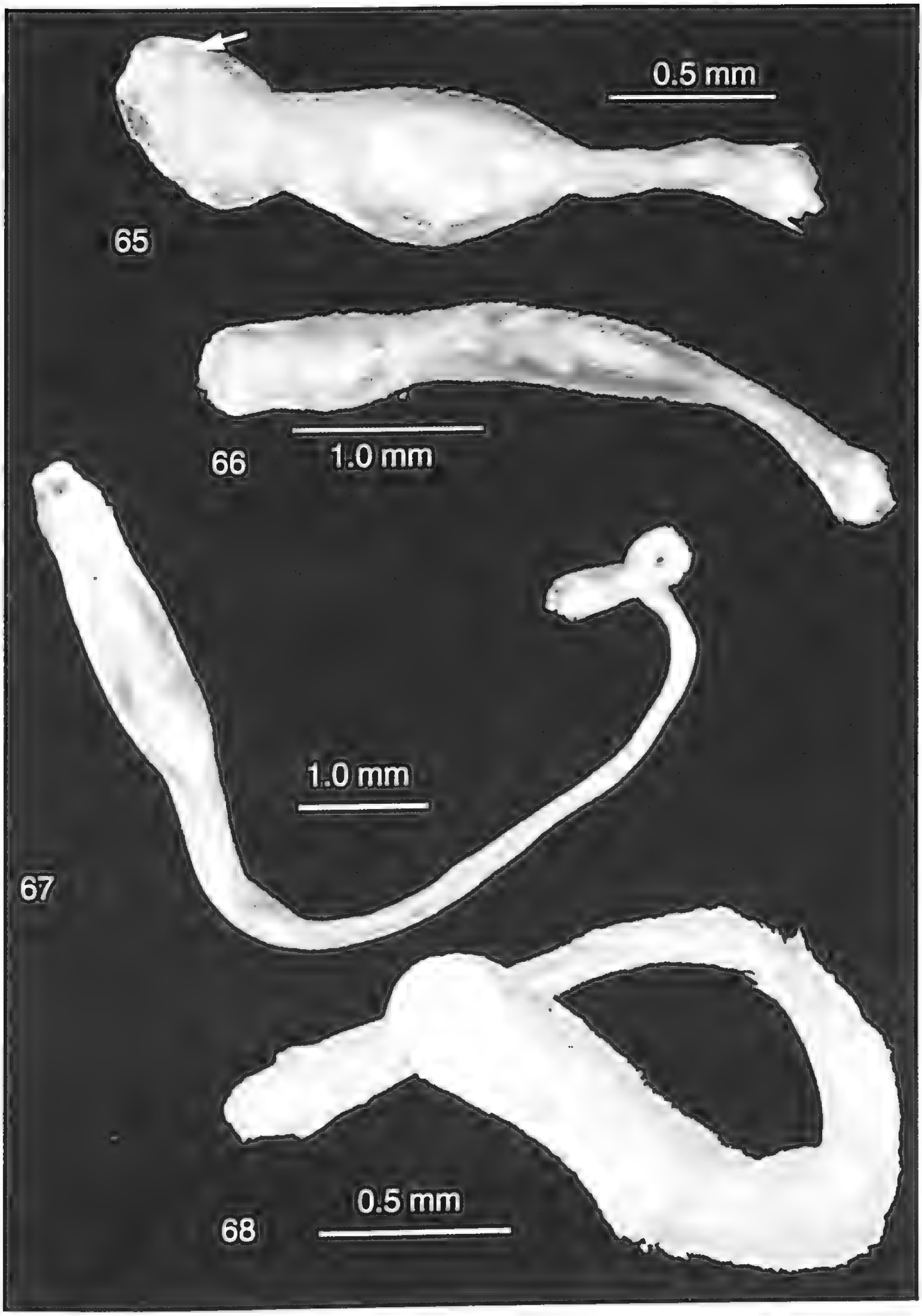
Elongate, semitranslucent, to nearly 5 mm in length, greatest diameter anterior, posterium 0.3 mm or greater, length posterium/trunk 0.68 or greater, spicules conspicuously long, shank spicules overlapping fringe spicules. Oral shield and oral shield spicules prominent on protruded anterium. Defining spicules long, slender, curved, with a broad thickening abfrontally appearing as a broad keel in transmitted light; trunk and shank spicules to 239 and 264 μm, respectively. Radula jaws to 660 μm long, 265 μm wide, teeth to 118 μm long, medial membrane with deep serrations.

Distribution (Fig. 69)

North-east of La Réunion Island at 3240 m (type locality) and northern Bay of Bengal (VITYAZ stn 4933; Table 1). The map published in Ivanov and Scheltema (2001*a*: fig. 18*b*) unfortunately places VITYAZ station 4933 off the west coast of India, although the coordinates are given correctly in the text and table. Two individuals (paratypes) were recorded from VITYAZ stn 4933 in that publication; the individual recorded here brings the total number to three at stn 4933. Our original description of individuals from La Réunion and the two paratypes from the Bay of Bengal were reported in Ivanov and Scheltema (2001*a*).

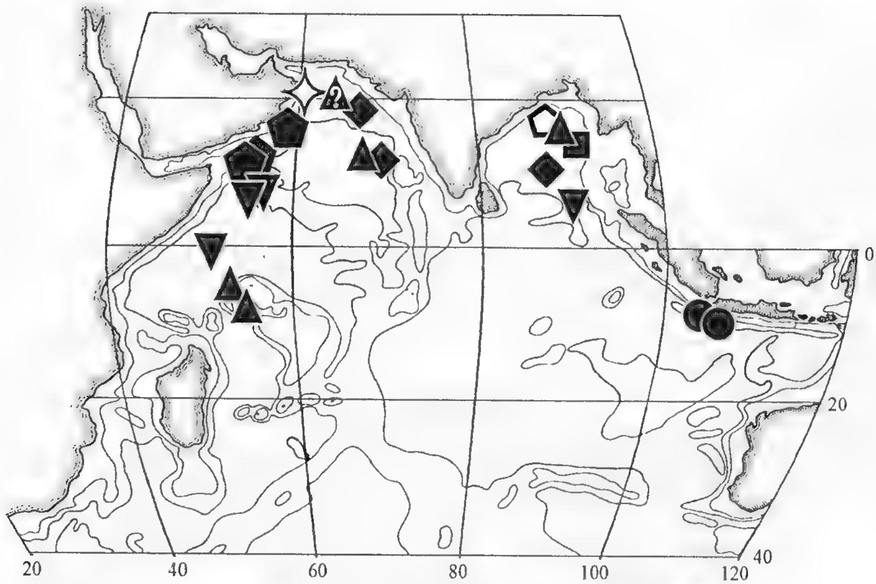
Discussion

All species of Prochaetodermatidae known from the Indian Ocean and Arabian Sea have been collected at depths below 1000 m (Table 2; Ivanov and Scheltema 2001*a*, table 1),



Figs 65–68. Holotypes of: *65*, *Prochaetoderma arabicum* n. sp., jaws (arrow) seen through cuticle; *66*, *Chevroderma lusae* n. sp.; *67*, *Chevroderma javanicum* n. sp.; and *68*, *Chevroderma vityazi* n. sp.

although a few Chaetodermidae (undescribed) have been found on the upper slope off La Réunion. It is uncertain whether the depth distributions reflect the actual situation or sampling effort.



Prochaetoderma: arabicum n. sp. (✧); *Chevroderma: turnerae* (▲), *javanicum* n. sp. (●), *lusae* n. sp. (◆), *vityazi* n. sp. (■), *paradoxum* (▼); *Claviderma: gagei* (⬟), *laticarinatum* (⬠).

Fig. 69. Map of species collected by the Soviet research vessel VITYAZ reported herein (Table 1).

The genus *Prochaetoderma* is represented by only two individuals of a single species, *P. arabicum*, in the Indian Ocean, yet one *Prochaetoderma* species, *P. yongei* Scheltema, is amphi-Atlantic and numerically dominant at some localities in the west Atlantic (Grassle

Table 2. Depth records for all known Indian Ocean/Arabian Sea prochaetodermatoid species

Species[A] and author	Sublittoral shelf 0–200 m	Bathyal Upper slope 200–1000 m	Bathyal Lower slope 1000–3000 m	Abyssal 3000–6000 m	Hadal >6000 m
S. subulatum Ivanov & Scheltema[B]			+		
S. longisquamosum (Salv.-Pl.)[C]			+		
P. arabicum n. sp.			+		
Chev. vityazi n. sp.			+		
Cl. laticarinatum Ivanov & Scheltema[B]				+	+
Chev. turnerae Scheltema[BD]			+	+	
Cl. gagei Ivanov & Scheltema[B]			+	+	
N. liliae Ivanov & Scheltema[B]			+	+	
Chev. paradoxum Ivanov & Scheltema[B]					+
Chev. lusae n. sp.				+	
Chev. javanicum n. sp.					+

[A]*Chev.*, *Chevroderma*; *Cl.*, *Claviderma*; *N.*, *Niteomica*; *P.*, *Prochaetoderma*; *S.*, *Spathoderma*.
[B]Ivanov and Scheltema, 2001*a*.
[C]Salvini-Plawen, 1986.
[D]Scheltema, 1985; Scheltema & Ivanov, 2000.

and Maciolek 1992). Species of other genera of Prochaetodermatidae are numerical dominants in the Aleutian Trench (*Chevroderma whitlatchi*; Scheltema 1985), eastern Pacific off California (*Spathoderma* sp.; Scheltema 1997) and western Atlantic (*Spathoderma clenchi*; Scheltema 1985; Grassle and Maciolek 1992). It has not been possible to determine densities of most populations of species in the Indian Ocean/Arabian Sea because samples have not been collected with quantitative gear. The only exception is for *Claviderma gagei* Ivanov & Scheltema, 2001, which were collected by 0.25 m^2 box cores in the west Arabian Sea, where densities were 28 m^{-2} at 3000 m.

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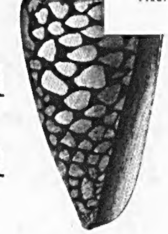

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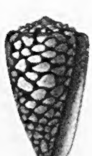

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